The application of biodiversity indicators to infer ecosystem health in regenerating tropical forest.

Laura Allen

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Institute of Biodiversity, Animal Health and Comparative Medicine
College of Medical, Veterinary and Life Sciences
University of Glasgow

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Abstract

There are an overwhelming number of biodiversity indices and indicators available for ecologists and conservationists to use when seeking to understand how biodiversity responds to human disturbance. In choosing between measures there is often an underlying assumption that if a measure works well for one group it will be equally applicable to another. In this study, I use multiple taxa to explore the performance of a wide range of alpha and beta diversity measures for studying biodiversity responses to human disturbance in tropical forest. I sampled 18 sites along a gradient of human disturbance from primary tropical forest to banana monocultures in Peru. I chose three taxonomic groups and one audio approach, which have all been suggested to be useful indicators for studying biodiversity responses to disturbance: orchid bees (n = 1783), dung beetles (n = 3787), butterflies (n = 2506) and soundscape samples (n = 6600). This allowed me to identify how these groups responded to disturbance, which diversity measures were most sensitive for detecting those changes and whether the same measures were suitable for all groups. I used Hill numbers to measure alpha diversity and explored beta diversity by looking at changes in community composition and two new measures of beta diversity: redundancy and representativeness. To see how the diversity patterns changed when taxonomic similarity was considered, I used a recently developed family of similarity-sensitive diversity measures and compared the results of these against more traditional measures. I found that the diversity indices that were best for detecting disturbance patterns varied widely among taxonomic groups. For dung beetles, species richness and community composition were the most effective measures, whereas these performed poorly for orchid bees. Abundance and redundancy were more sensitive for detecting a response to disturbance in orchid bees. Using the butterfly dataset, I show that the inclusion of species similarity completely changed the diversity patterns found across the disturbance gradient. The similarity of species present in a community is likely to be important for the preservation of evolutionary adaptability and the provision of ecosystem functions and I therefore suggest that diversity measures based on similarity will be a useful additional tool for conservation and impact assessments. Acoustic diversity showed unintuitive responses to disturbance, with higher diversity detected in more disturbed forest, and more research is

required to assess the performance of different acoustic indices in rainforest environments. Overall, my results demonstrate the importance of choosing diversity indices carefully to suit the taxa being studied to avoid missing important ecological responses, including a consideration of species similarity. I recommend that, where possible, multiple diversity indices and taxonomic groups should be used to reduce this risk and provide a comprehensive understanding of ecosystem patterns in response to environmental change.

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Author's declaration

I declare that this thesis is the result of my own work, except where explicit reference is made to the contribution of others. No part of this work has been submitted for any other degree or qualification. This research was conducted between October 2014 and June 2018, under the supervision of Dr Ross Macleod, Dr Richard Reeve and Dr Anna McGregor.

Laura Allen

1 General Introduction

1.1 Tropical forests and their conservation

Tropical rainforests occur in a band around the Equator, with key blocks in South America, West and Central Africa, and South-East Asia (Whitmore, 1998). They have a warm and wet climate with little seasonal variation and the vegetation is highly diverse, with a high canopy of large trees and layered understorey creating a complex three-dimensional habitat (Whitmore, 1998; Figure 1.1). Around 7% of the Earth's land surface is covered by tropical rainforest but these forests are home to more than 60% of the world's species (Bradshaw, Sodhi & Brook 2009). Of all the terrestrial ecosystems, tropical rainforests are the most biologically diverse and ecologically complex (Laurance 2006), and provide a wide range of ecosystem functions and services important for life on Earth (Lewis *et al*. 2013). The high biodiversity of tropical forests is thought to be due to several factors, including their long evolutionary history with extensive periods of relatively stable climatic conditions (Peres *et al*. 2010), high temperatures and plenty of sunlight creating a resource rich environment enabling rapid ecological and evolutionary processes (Brown 2014), and high speciation of consumers as a result of high primary producer diversity (Novotny *et al*. 2006). Approximately one million species are currently known from tropical forests around the world (Wilson 2013), but it is estimated that we have many more yet to identify (Wilson 1987; May 1990; Magurran 2004). As well as being home to the most species of plants and animals, genomic, taxonomic and even cultural diversity are also highest in the tropics (Brown 2014), making it a truly remarkable place, deserving protection.

Figure 1.1 Tropical forest on the banks of the Alto Madre de Dios in the cultural zone of the Manu Biosphere Reserve, Peru.

Tropical rainforests are threatened by a range of pressures, including logging for timber (Figure 1.2), clearance for agriculture and pollution from mineral extraction (Chazdon *et al*. 2009). Overall, the largest threat to tropical rainforests globally is habitat loss and degradation, followed by overexploitation (including hunting for bushmeat), invasive species, disease, pollution and climate change (WWF 2016). Although all of these threats are globally important, there is regional variation in their impacts, with forest clearance for palm-oil being the most dominant threat in South-east Asia, whereas in South America, clearance for cattle ranching is a bigger problem, and bushmeat hunting is particularly intense in West Africa (Bradshaw, Sodhi & Brook 2009). The impacts of hunting for bushmeat can have several negative consequences for the integrity of the ecosystem, include reducing the prey availability for large carnivores, and impacting seed dispersal functions provided by frugivorous species. Activities that result in destruction of forest habitat include conversion of the land for agriculture and livestock, the creation of roads and activities associated with increased access, and logging. Different logging methods exist, including clear cutting, which removes trees from complete tracts of land, and selective logging which targets only large trees of key species. However,

although selective logging is less destructive than clear cutting (Burivalova, Şekercioğlu & Koh 2014), the roads and machinery required to remove these trees, as well as the removal of important large trees from the system, means that the impact can still be considerable. Agricultural techniques vary widely, and, in some areas, agriculture is conducted on a large scale with strict monocultures of species, as is often the case with palm oil. This frequently takes place on land that was cleared of pristine forest, with heavy consequences for biodiversity in those areas (Lees *et al*. 2015). In many places, agriculture is performed at a much smaller scale, with farmers growing enough for personal use and for a small income. This is quite often dominated by one crop, such as banana or pineapple in Amazonia, but with a few additional species mixed in. Efforts have been made to reduce environmental impacts through improvements in agriculture, such as with shade coffee (Perfecto *et al*. 1996) or agroforestry, where crops are interspersed with native timber species that can be harvested for wood and thereby reduce logging pressure. The additional trees in these agroforestry plantations provide resources that may help to support biodiversity and ecosystem services, as well as shade and nutrients that directly benefit the crops (Montagnini *et al*. 2005).

It is estimated that currently about three quarters of the world's forests have been in some way impacted by humans and can no longer be classed as pristine (Food and Agriculture Organisation of the United Nations 2015). Rates of forest loss remain high worldwide, with an estimated 31 million ha of primary forest cleared or modified since the 1990s, and only 26% of current forest cover considered primary (FAO, 2015). In some areas forest cover has increased, with secondary forest and plantations partially offsetting some of the total forest cover lost. However, these do not match the structure and composition of the original primary forest and cannot be considered equivalent in terms of their value for the conservation of biodiversity or ecosystem functioning (Wright 2005; Chazdon 2008; Tabarelli *et al*. 2010). As the human population continues to increase, agriculture in tropical regions is predicted to expand, as is secondary forest regenerating on abandoned degraded land (Wright 2005). Protected old growth forest is likely to persist in isolated patches within this matrix of secondary and agricultural land. It is therefore important to understand how biodiversity and ecosystem functions persist in such landscapes, and how we can

manage the land in order to protect the remaining old growth forest and the species within it.

Figure 1.2 Logging of large hardwoods is a big threat to tropical forests in the Manu region. This was taken in the Amarakaeri communal reserve close to our research station.

There are several important considerations when assessing the responses of biodiversity to tropical forest disturbance: the type and intensity of disturbance, which species or groups of species are involved, and what response measure is used (Gibson *et al*. 2011). Logging and conversion to agriculture have both been associated with reduced species richness compared to intact forest (Burivalova, Şekercioğlu & Koh 2014), and the more severe the disturbance, the greater the loss of species. Some types of agriculture have been found to sustain higher levels of biodiversity than others, such as rubber compared to oil-palm (Peh *et al*. 2006). Species richness of birds has been found to show little response to forest disturbance compared to some other taxa. However, species composition of the bird community was more sensitive, with a loss of forest species and an increase in generalist and open habitat species (Edwards *et al*. 2010; Catterall *et al*. 2012). Some traits may also make particular species more vulnerable to extinction, such as their reproductive strategy, thermal limits or mutualistic relationships (Stork *et al*. 2009).

Overwhelmingly, the impacts of tropical forest disturbance on biodiversity are negative (Gibson *et al*. 2011), but there are some options for mitigating the severity of these impacts and for identifying land management strategies that can help to protect biodiversity. Research into the impacts of forest disturbance and regeneration on biodiversity is a vital step in this process. There is potential for biodiversity and ecosystem functions to recover if disturbed land is allowed to regenerate, but the success of this recovery depends on several factors, including soil fertility, patch size, restoration methods, prior land use intensity and proximity to primary forest for source populations (Chazdon 2003; Jakovac *et al*. 2015; Whitworth *et al*. 2016b). Species richness of many taxa may reach comparable levels to old-growth forest within a relatively short time, but community composition can be much more difficult to recover (Catterall *et al*. 2012).

1.2 Biodiversity monitoring

Biodiversity is a term used to describe all the variety of life found on Earth. The diversity of life can be considered at multiple levels, but the unit most often used is species-level diversity (Magurran 2004). This diversity has evolved over billions of years, with species adapting to fill different niches including specialisations in habitat, diet, body-size, activity times and different environments. As a result there has been an overall increase in biodiversity over geological time, interrupted by a small number of mass extinction events that reduced the number of species and led to alterations of the dominant communities (Dirzo & Raven 2003). The best known of these extinctions are the Permian-Triassic, which is the largest extinction event in Earth's history, and the Cretaceous-Tertiary, which led to the extinction of the dinosaurs. However, there is evidence that we are now in the middle of a sixth mass extinction, where human activity, including climate change and habitat destruction, is leading to a loss of species at more than 100 times the background extinction rate (Ceballos *et al*. 2015; Ceballos, Ehrlich & Dirzo 2017). The impact of human activities on the Earth's ecosystems is so vast that it has been recognised as a new era, the Anthropocene (Dirzo & Raven 2003; Lewis & Maslin 2015).

To protect biodiversity, we need to know what species exist and where, and we need to be able to assess how that changes in response to different types of

418 disturbance over space or time (Villalobos *et al*. 2013). Therefore, monitoring
419 biodiversity is a key activity in ecology and conservation. Monitoring biodiversity
420 provides insight into trends that can inform us about the health of an ecosystem,
421 and make informed decisions on resource use and the protection of land and
422 species (WWF 2016). The future of tropical ecosystems and their component
423 species depends on their effective management, so we need to monitor the
424 biodiversity of a site to be able to identify the impacts of conservation strategies
425 or potential disturbance events (Gardner *et al*. 2009). A shortage of resources,
426 including both expertise and funding, means that it is necessary to prioritise
427 areas for conservation; monitoring biodiversity is useful for identifying areas of
428 high conservation value (Myers *et al*. 2000; Moilanen *et al*. 2005).

429 The loss of biodiversity is important for many reasons, including both moral and
430 utilitarian values (Laurance 1999; Pearson 2016). It has been argued that nature
431 has intrinsic value and therefore we have a moral obligation to protect it, which
432 is a worthwhile philosophical and ethical consideration (Ghilarov 2000; Batavia &
433 Nelson 2017). Although it cannot be proven, we can generally agree that a
434 diversity of organisms is good, and that the untimely extinction of populations
435 and species is bad (Soulé 1985). Other species have value regardless of their
436 contributions to people, and a right to existence; we have a moral duty to
437 protect these species and to ensure we don't contribute to their untimely
438 demise (Carafo & Primack 2014). Furthermore, we are still in the preliminary
439 stages of understanding life on Earth, and we have yet to discover or describe a
440 substantial proportion of the species that exist (May 1990), never mind even
441 come close to understanding how those species interact with one another or
442 with the environment (Bennett, Peterson & Gordon 2009). Once species go
443 extinct, there is no going back, and millions of years of evolutionary adaptation
444 may be lost forever (Dirzo & Raven 2003). It seems incredibly reckless to allow
445 the loss of these species and habitats before we even understand what is there
446 or exactly how important they are, as well as being ethically unacceptable.
447 However, we do know that biodiversity is important for the maintenance of
448 many ecosystem functions, which are vital for the persistence of the ecosystems
449 themselves (Hooper *et al*. 2005). In the interest of self-preservation, biodiversity
450 is also essential for the delivery of ecosystem services, the subset of ecosystem
451 functions that directly benefit humankind, such as flood control or crop

pollination (Daily *et al*. 1999). High biodiversity not only provides a wide range of ecosystem functions, but also a degree of functional redundancy that can make ecosystems more resilient to disturbance (Hooper *et al*. 2005). If we lose the component species of an ecosystem we lose the functions they perform, which may lead to ecosystem collapse and severe consequences for the people and wildlife that depend on them (Laurance 1999). It is therefore essential that we maintain high biodiversity at multiple levels; ensuring that species, populations and ecosystems are preserved.

1.3 Biodiversity and ecosystem functions

Ecosystem functions are the biological, geochemical and physical processes and the interactions between organisms and the environment that operate within an ecosystem and help to sustain it (Jax 2005; Edwards *et al*. 2014). Key ecosystem functions include nutrient cycling, seed dispersal, decomposition and many other interactions within and between the structural components of an ecosystem, including the water, soil, atmosphere, plants, microbes and other organisms (Figure 1.3). The terms ecosystem function and ecosystem services are often used interchangeably, but ecosystem functions can be considered of importance independent of their contribution to human wellbeing, whereas ecosystem services are the often considered as the subset of ecosystem functions that are of value to humans, such as carbon-storage, crop pollination, erosion control and opportunities for recreational activities (Daily *et al*. 1999; Jax 2005).

Figure 1.3 A Euglossine bee visiting an orchid at the Manu Learning Centre. These bees have a highly specialised mutualistic relationship with orchids, which depend on them for pollination (Photo by Jack Mortimer, 2015).

The delivery of ecosystem functions relies on the various components of the ecosystem that fill distinct roles. This means that the variety of species present in the ecosystem has an important part to play in ecosystem functioning. Several studies have shown a clear relationship between biodiversity and ecosystem functioning (Balvanera et al., 2006). Higher biodiversity is related to higher productivity and a more stable supply of ecosystem goods and services, as well as reduced vulnerability to invasion and disturbances (Tilman, Wedin & Knops 1996; Hooper *et al*. 2005). In simple terms, the greater variety of species present, the more functional groups will be represented and the wider range of functions they will be able to carry out. Additionally, complementarity among species can further increase process rates (Slade *et al*. 2007), as well as providing a degree of redundancy that can reduce the sensitivity of an ecosystem to disturbance events (Hooper *et al*. 2005). Unfortunately, despite the essential nature of ecosystem functions and services, human alteration of natural landscapes has led to a decline in many of these (Hooper *et al*. 2005; Bennett, Peterson & Gordon 2009), with severe consequences for the persistence of important habitats as well as the services that we rely on. Conservation efforts must take ecosystem functions as well as biodiversity into consideration. The two are not always perfectly correlated (Naidoo *et al*. 2008) and may

operate at different scales, or the relationship may depend on the taxa, ecosystem type and diversity measure used (Balvanera *et al*. 2006). However, substantial concordance between biodiversity and ecosystem functioning means that choosing conservation priority areas based on maximising biodiversity will also provide substantial benefits for ecosystem functioning, making efficient use of limited conservation resources (Turner *et al*. 2007; Naidoo *et al*. 2008).

1.4 Indicators

Ecosystem functions can be very challenging to quantify (Müller & Burkhard 2012), and this often involves time consuming experiments in controlled environments (Naeem & Wright 2003; Hoppe *et al*. 2016; Steudel *et al*. 2016; Baumann *et al*. 2017). These types of experiments are essential for establishing an understanding about the relationship between functions and several aspects of biodiversity, including the effects of specific species, assemblages and environmental conditions. However, this approach is often not feasible for use in rapid assessment of areas for the establishment of conservation priorities or for regular monitoring of sites over time. Therefore, we need some efficient way of measuring some property of the ecosystem that will provide an indication of the state of individual ecosystem functions or of the overall health of the ecosystem. The same is true for biodiversity, especially in the tropics, where data are sparse and diversity is high (Ghazoul & Sheil 2010). Instead we aim to sample part of the community that will provide us with a reasonable estimate of the biodiversity that might exist at that site (Magurran 2004). Ideally, we want a measure that will correlate well with overall biodiversity and functioning, and be easy and cost-effective to quantify (Gardner *et al*. 2008a).

One of the most common approaches to rapid assessment and monitoring of biodiversity and ecosystem health is the use of surrogate taxa. There are several types of surrogates, including keystone species, umbrella and flagship species and indicator taxa. Keystone species are those which play an outsized role in the ecosystem, such as the wildebeest (*Connochaetes taurinus*) of the Serengeti (Borner *et al*. 2010). Umbrella species are those with a large range, therefore protecting that area will also benefit all the other species that share their habitat requirements, whereas flagship species hold charismatic appeal that attracts funding (Walpole & Leader-Williams 2002), which can also confer

conservation benefits to other species, a classic example being the giant panda (*Ailuropoda melanoleuca*) (Li & Pimm 2016). Indicator species or groups are those that can provide an indirect measure of a quantity of interest (Fleishman & Murphy 2009), such as total biodiversity, the biodiversity of a specific taxonomic group, the health of the ecosystem or pollution levels. Indicators clearly have the potential to be very helpful in conservation planning and ecological assessments, so it is unsurprising that they are widely used. However, there is some concern about their application and what they are used to indicate.

There has been a substantial effort made to define what makes a good indicator. Some of the key features required are that the indicator should be widespread, common, easy to sample and show a strong and consistent response to the indicandum (Brown 1997; Favila & Halffter 1997; Gardner *et al*. 2008a; Goodsell, Underwood & Chapman 2009). However, one of the key problems with the use of indicators is a lack of clarity as to what they indicate. Some examples of indicator uses discussed earlier include: specific functions, e.g. pollination; overall ecosystem health, which is difficult to define, never mind measure (Kolasa & Pickett 1992; Rapport, Costanza & McMichael 1998; Jax 2005); or overall biodiversity (Mac Nally & Fleishman 2002). Other uses in the literature include the assessment of water quality (Mauricio da Rocha *et al*. 2010), pollution (Giordani 2007), restoration success (Jansen 1997) and responses to climate change (Hill *et al*. 2002). Therefore, an important starting point in indicator selection should be identifying what it is you want it to indicate, and then proceed with a stepwise selection of taxa based on other important criteria (Hilty & Merenlender 2000).

Despite the convenience of using indicators to infer habitat quality or conservation value, too often the taxa used as indicators do not fulfil many of the requirements identified as key features of good indicators. A lack of congruence in the responses of common indicator groups with other taxa suggests that they cannot necessarily be reliably used to infer general biodiversity responses (Lawton *et al*. 1998; Ricketts, Daily & Ehrlich 2002; Barlow *et al*. 2007a). It is also often unclear as to how well indicators represent ecosystem health or other trends, with relationships often assumed rather than tested (Hilty & Merenlender 2000). The congruence between groups may depend

562 on the choice of diversity metric, with community similarity and composition
563 suggested to perform better than the more commonly used species richness (Su
564 *et al*. 2004; Stork *et al*. 2017). The performance of indicators can also vary with
565 scale and geographic region, meaning that indicators developed under one set of
566 conditions may not be suitable at other grains or locations (Hess *et al*. 2006).

567 Indicators can help to detect a biotic response to an environmental change and
568 provide an early warning of the impacts of environmental stress; however, the
569 role of indicators in this context is only useful for measuring changes that are
570 difficult to detect directly (Kremen 1992). An indicator is only valuable if it is an
571 accurate, cost-effective, efficient method of assessing more complex
572 environmental characteristics and the assessment target is clearly defined
573 (Fleishman & Murphy 2009). In this study, I investigate multiple groups that
574 could potentially be used as indicators of biodiversity responses to disturbance
575 or changes in some ecosystem functions. The use of these groups as indicators is
576 part of the motivation for the study. However, my aim was not to test how well
577 these groups represent biodiversity or function. Instead I have focused on what
578 trends these groups show in response to disturbance and what biodiversity
579 measurement approaches are most sensitive for detecting these changes. This
580 provides evidence that can be useful for anyone applying these groups for
581 ecological assessment or monitoring and highlights some important
582 considerations for using these potential indicators.

1.5 Quantifying biodiversity

It is not feasible to measure the total biodiversity of a site, especially not in tropical forests, due to the high number of species present (Figure 1.4), taxonomic uncertainty, the number of undescribed species, and the difficulty in detecting many species (Gotelli & Colwell 2001; Basset *et al*. 2004; Ghazoul & Sheil 2010). Therefore, our conclusions as to the biological richness of a site must be based on samples. There are several important steps in this process – the first is to clearly identify the goal of the study (Sutherland, 2006). Then, based on this, decide what to survey, how to collect the data, and then carry out the data collection, which often includes adapting to unforeseen circumstances along the way. The collected data can then be used in analyses that attempt to quantify or estimate the diversity present.

Figure 1.4 *Siphlophis cervinus*, one of over 60 reptiles found within the Manu Learning Centre reserve (Whitworth *et al.* 2016b), where this research was conducted.

Deciding what you are going to sample and how is a key decision, as it has implications for study results. This is where surrogate groups and indicators might come in, or there may be species or groups that are of special scientific interest or conservation concern in a region. Unless the aim of the study is to learn about the biology of a little studied group, the ease of sampling and identification of the chosen target may be important to consider for survey

efficiency (Gardner et al., 2008). Depending on what you are collecting data on, the most appropriate method for data collection is likely to differ (Figure 1.5). It is essential to set up a careful sampling design in advance, to ensure proper coverage of the areas and adequate sampling effort, and to avoid issues such as pseudoreplication (Hurlbert 1984; Sutherland 2006). Some common survey methods used in tropical forest include line transects (Linder & Oates 2011), visual encounter surveys (Whitworth *et al*. 2017), point counts (Haselmayer & Quinn 2000), pitfall trapping (Hayes *et al*. 2009) and camera traps (Whitworth *et al*. 2016a), but there are many more specialised approaches depending on the target species. Advances in technology have also opened the doors for more sophisticated methods of remote sensing (Peres, Barlow & Laurance 2006), such as the use of LiDAR and related methods (Turner *et al*. 2003; Müller & Brandl 2009; Pekin *et al*. 2012; Thers *et al*. 2017) and acoustic monitoring (Rodriguez *et al*. 2014) as well as automated species identification (Jennings, Parsons & Pocock 2008).

Figure 1.5 Some of the sampling methods used in this study include butterfly trapping using Van Someran traps (left) and baited pitfall traps for dung beetles (right).

Once the data have been collected, the next challenge is how to analyse them. There are an enormous number of ways to quantify biodiversity, which has led to difficulties in comparing the results of studies, as well as confusion by practitioners as to what metrics to use. Part of the problem is in identifying

what sort of diversity we care about and how we value different contributions to diversity; fundamentally these problems of calculating diversity are not specific to biology, but are shared across fields, including economics, culture and psychology (Gravel 2009). Within ecology and conservation, another problem lies in clearly defining what sort of diversity is being discussed in a study and why (Spellerberg & Fedor 2003; Hill *et al*. 2016; Socolar *et al*. 2016; Stork *et al*. 2017).

Biodiversity can be categorised into three basic components: alpha diversity, which is the diversity of a single site or subcommunity within the system; beta diversity, which is the difference in diversity between sites; and gamma diversity, which is the total diversity of all the different sites present in the metacommunity (Chao, Chiu & Hsieh 2012; Reeve *et al*. 2016). Each of these three aspects of diversity can be quantified in a number of different ways. However, it is desirable that there should be some unified mathematic theory relating them to one another (Chao, Chiu & Jost 2014; Reeve *et al*. 2016). The most commonly used method of estimating alpha diversity is species richness – this is intuitive, easy to understand and has been applied to a broad range of ecological problems (Gillespie *et al*. 2005; Király *et al*. 2012; Linden *et al*. 2014). However, even simple species richness can be estimated by several formulae (Gotelli & Colwell 2011; Reese, Wilson & Flather 2014), and it is a measure that is highly sensitive to the presence of rare species. Other indices, such as the Shannon and Simpson indices, take into account the relative abundance of species, and place less weight on species that are rare in the community (Shannon 1948; Simpson 1949; Magurran 2004). Recent discussions have concluded that a unified framework of diversity using effective numbers is a suitable approach to partitioning diversity (Chao, Chiu & Hsieh 2012). Effective numbers enable easy comparison of multiple calculations of diversity depending on the weight given to rare species in the samples (Hill 1973).

Beta diversity is a measure of comparison between sites and has the greatest variety of indices for its measurement (Tuomisto 2010). Recent mathematical advances have extended the effective numbers approach to work with beta diversity, resulting in a common framework for partitioning diversity into its alpha, beta and gamma components (Reeve *et al*. 2016). Within this framework, beta diversity can be used at both the subcommunity and metacommunity levels

659 to understand the distinctiveness and redundancy of the communities, that is
660 how the community of a site compares with the overall biodiversity of the area
661 in terms of the species found there. Other approaches to beta diversity
662 measurement focus on community composition and similarity. Community
663 composition focuses our attention on what species are present, rather than only
664 the number and abundance of species. This is an important consideration, as
665 some species are of greater conservation concern or have highly specialised roles
666 in the ecosystem, and therefore their loss may have a bigger impact than the
667 loss of other species. Comparing the community similarity between sites or
668 timepoints can be an effective way of assessing disturbance or recovery (Volio *et*
669 *al*. 2015; Socolar *et al*. 2016), but may depend on availability of data on the
670 'ideal' target community, such as a nearby primary forest site or pre-
671 disturbance baseline data.

672 Further extensions of biodiversity measurement include the consideration of
673 species similarity within diversity indices (Shimatani 2001), as well as re-
674 directing attention away from species level diversity and concentrating instead
675 on other types, such as genetic and functional diversity (Bengtsson 1998; Jarzyna
676 & Jetz 2016). Traditionally, species diversity measures have treated all species
677 in a community as equally distinct from one another, but we know that is not
678 the case (Bengtsson 1998; Shimatani 2001). Species may share similar diets,
679 habitat preferences or a more recent evolutionary divergence, any of which
680 might be important in conservation or ecological contexts. These similarities can
681 now be incorporated into the calculation of community diversity at the alpha,
682 beta and gamma level (Leinster & Cobbold 2012; Reeve *et al*. 2016), providing
683 further information with which to study changes in communities and to inform
684 conservation priorities. Other important advances in diversity measurement are
685 the development of methods of quantifying functional and genetic diversity.
686 Functional diversity can be used to understand how many different functional
687 traits are present in an ecosystem, such as different feeding guilds or leaf size.
688 Functional diversity is thought to relate more closely with ecosystem
689 functioning, but it can be challenging to decide what functional traits to
690 consider and how to measure their diversity (Petchey & Gaston 2006). Genetic
691 diversity has provided valuable evidence for understanding disease resistance
692 (Zhu *et al*. 2000; Rasmussen *et al*. 2014) and for the conservation of vulnerable

species (Hendricks *et al*. 2017; Austin *et al*. 2018). Genetic diversity has also become a valuable approach for distinguishing between morphologically similar cryptic species, which have long been a challenge for biodiversity assessments (Hebert *et al*. 2004; Bickford *et al*. 2007), although establishing the thresholds for species boundaries remains difficult.

Measuring biodiversity is a complex task and crucial for the assessment and monitoring of natural habitats and their responses to environmental change. Choice of diversity measure really does matter, and several studies have found that the choice of diversity metric can make a difference as to whether a change in a community is detected. Different types of diversity may differ in their detectability and vary differently along spatial and environmental gradients (Jarzyna & Jetz 2016). Some indices work better for detecting particular types of community change than others, and few perform consistently well under different circumstances (Santini *et al*. 2017). It is possible for alpha diversity measures to show little change, whereas beta diversity measures could reveal important underlying changes occurring in the community composition (Socolar *et al*. 2016; Magurran *et al*. 2018). These apparent discrepancies between diversity measures make sense, since the measures were developed for different purposes, but it is also worrying, since many studies only examine diversity patterns using one or two measures, which risks overlooking important trends. Increasingly researchers are recommending the careful selection of diversity measures and the application of multiple diversity measures to address this problem (Socolar *et al*. 2016; De Palma *et al*. 2017; Santini *et al*. 2017; Stork *et al*. 2017).

1.6 Thesis aims and structure

The overall aims of this thesis are to investigate how biodiversity responds across a gradient of human disturbance in an agricultural-forest landscape in Peru and to assess how the choice of biodiversity index can influence the detection of biodiversity responses. Biodiversity is assessed using multiple approaches, including several proposed indicator taxa as well as soundscape methods, providing the opportunity to understand how different groups respond to the same disturbance pressures, and whether the most suitable diversity metrics are shared across the groups.

The structure of this thesis is a general introductory chapter followed by four data chapters, each focusing on the responses of a group (taxon or soundscape), finishing with a final discussion chapter. All statistical tables and additional figures that may be of interest are included in the appendices. The topics and aims of each chapter are described below:

Chapter 1 General introduction.
An overview of tropical rainforest conservation relevant to the challenges of measuring biodiversity, including the use of indicators and diversity metrics, as well as an introduction to the study site and research aims.

Chapter 2 Study Area
An introduction to the region where this study was conducted, including a description of the study sites and information on their disturbance history and vegetation structure.

Chapter 3 Dung beetles as indicators: what we measure matters.
I studied the responses of the dung beetle assemblages across a gradient of disturbance, with the aim of identifying how dung beetles respond to this disturbance gradient and which measures of dung beetle diversity are most sensitive for detecting their responses. I also evaluate changes in some ecosystem functions provided by dung beetles across the disturbance gradient.

Chapter 4 Orchid bee responses to human disturbance are better detected using redundancy and abundance.
In this chapter I identified how orchid bees responded to human disturbance along the study gradient, and which measures of diversity were most sensitive for detecting changes in the community, including testing the application of two novel measures of beta diversity. To put this in the context of what the consequences might be for ecosystem function, I also assessed the potential pollination services available along the gradient by looking at general pollinator visitation rates at artificial flowers.

Chapter 5 Exploring the use of similarity-sensitive diversity measures for detecting the impacts of human disturbance: a case study on neotropical butterflies.

I investigated how butterfly diversity changes across a human land use gradient in tropical forest and tested how recently developed diversity measures can help to detect and explore these responses. I also explored if recent advances in similarity-sensitive biodiversity measurement can add valuable insights into patterns of biodiversity change in response to human disturbance and consider the implications of this for conservation.

Chapter 6 Using soundscape diversity to assess the impacts of human disturbance on tropical forest biodiversity.

In this chapter I investigated whether acoustic diversity measures are a useful method for detecting a response by the biological communities across a gradient of human disturbance in regenerating tropical forest in Peru, including the comparison of three commonly used acoustic indices.

Chapter 7 Discussion.

The findings of the four data chapters are brought together and discussed in the context of one another, as well as in the light of other studies in the published literature.

2 Study area

2.1 Introduction

The research presented in this thesis was conducted in the Amazon rainforest, in the Manu region of Southeast Peru (12°47'23.6" S, 71°23'30.3" W, Figure 2.1). The Amazon is the largest area of tropical rainforest in the world, and the most species-rich (Peres *et al*. 2010; Antonelli *et al*. 2018). However, despite the importance of the region, protected areas in the Amazon and in Peru only partially protect the rich biological diversity of the area, and even these remain vulnerable (Yu, Hendrickson & Castillo 1997; Rodríguez & Young 2000; Schulman *et al*. 2007). The Manu Biosphere Reserve, which includes the national park and cultural buffer zone is a UNESCO world heritage site and has been recognised as a global hotspot for biodiversity (Lamas, Robbins & Harvey 1991; Patterson *et al*. 1998; Patterson, Stotz & Solari 2006; Catenazzi, Lehr & Von May 2013). This work took place in the cultural zone of the biosphere reserve, in and around the Manu Learning Centre, a research and ecotourism centre on the northern bank of the Alto Madre de Dios river. The study site sits within a matrix of land uses, surrounded by a mixture of intact tropical forest, areas of intermediate disturbance, agricultural land and small settlements. It is a good representation of typical land use in the region, and therefore an ideal location to study the relationship between human disturbance and biodiversity in this context (Whitworth *et al*. 2016b, 2016c, 2018).

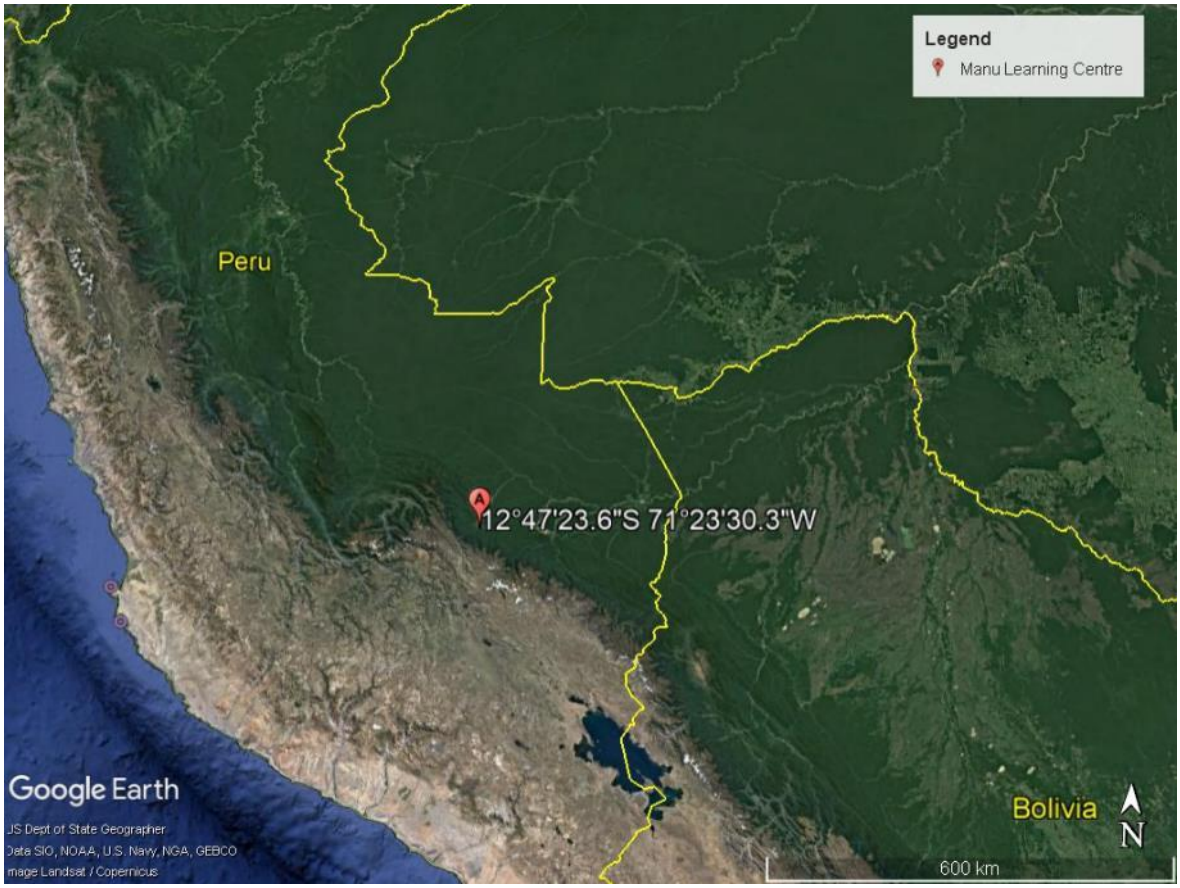

Figure 2.1 Map of Peru showing the location of the study site, the Manu Learning Centre.

The Manu Learning Centre is a private reserve, which has been protected for over 30 years and contains a mix of near-pristine and regenerating forest. The reserve once contained a cattle ranch, so some areas were completely cleared for livestock, but this has since regrown into closed-canopy forest (Figure 2.2d). Other parts of the reserve were partially cleared for small scale agriculture, with plantations of coffee and cacao, and these areas have also regrown (Figure 2.2e). The least disturbed part of the reserve has not to my knowledge ever been cut down; it is possible that a few large trees may have been removed for timber, but many large trees remain (Figure 2.2f). Within the same river valley, on the other side of the Alto Madre de Dios river, lies a small road that runs from the nearby town of Salvación (population approximately 2000 (Lin 2015)) to some of the small native communities downriver. The land around the road has been almost completely cleared of forest for several kilometres and is dominated by plantations of banana plants, either in exposed fields cleared of all other vegetation (Figure 2.2a), or in agroforestry plots (Figure 2.2b). Agroforestry plots have become popular in the area through the support of several organisations, including the Crees Foundation. They combine banana plantations with native timber species, including both fast growing softwoods as

well as hardwood species. This mix of species provides shade and a complex vegetation structure, which it is hoped will benefit wildlife as well as shading the crops and improving soil quality. Additionally, the trees can be harvested when timber is needed, reducing logging pressure on nearby forests. At the borders of many plantations are areas of secondary forest that have grown up on land cleared in the recent past but not under current production (Figure 2.2c). These areas generally have partial canopy cover, dense understorey vegetation and exist in small patches. The sites used in the studies presented here cover a gradient from the near-pristine forest in the Manu Learning Centre to the most exposed plantations of banana monocultures. The agroforestry plots, recent secondary forest and the areas of regenerating forest at the Manu Learning Centre provide intermediate levels of disturbance along the gradient. The land uses of the sites were classified by a combination of local knowledge, previous research conducted in the area (Whitworth *et al.* 2016c), and vegetation structure assessments, as well as first hand inspection of the sites. The study sites cover a region of around 20km^2, which means it is large enough to provide a satisfactory distance between sites of the same disturbance type and to intersperse sites of the different types, but it is still small enough that it is highly likely that the vegetation cover and biological communities across the area would have been very similar prior to human disturbance. The cultural zone of the Manu Biosphere Reserve is important because it provides a protective buffer to the national park and holds very high biodiversity but is subjected to many more threats than the strictly protected national park, including logging, tourism, roads and urbanisation. Therefore, gaining a better understanding of how biodiversity responds to human disturbance in this region and how to monitor these changes effectively can provide evidence for land management strategies that meet the needs of local people and protect this globally important hotspot of biodiversity.

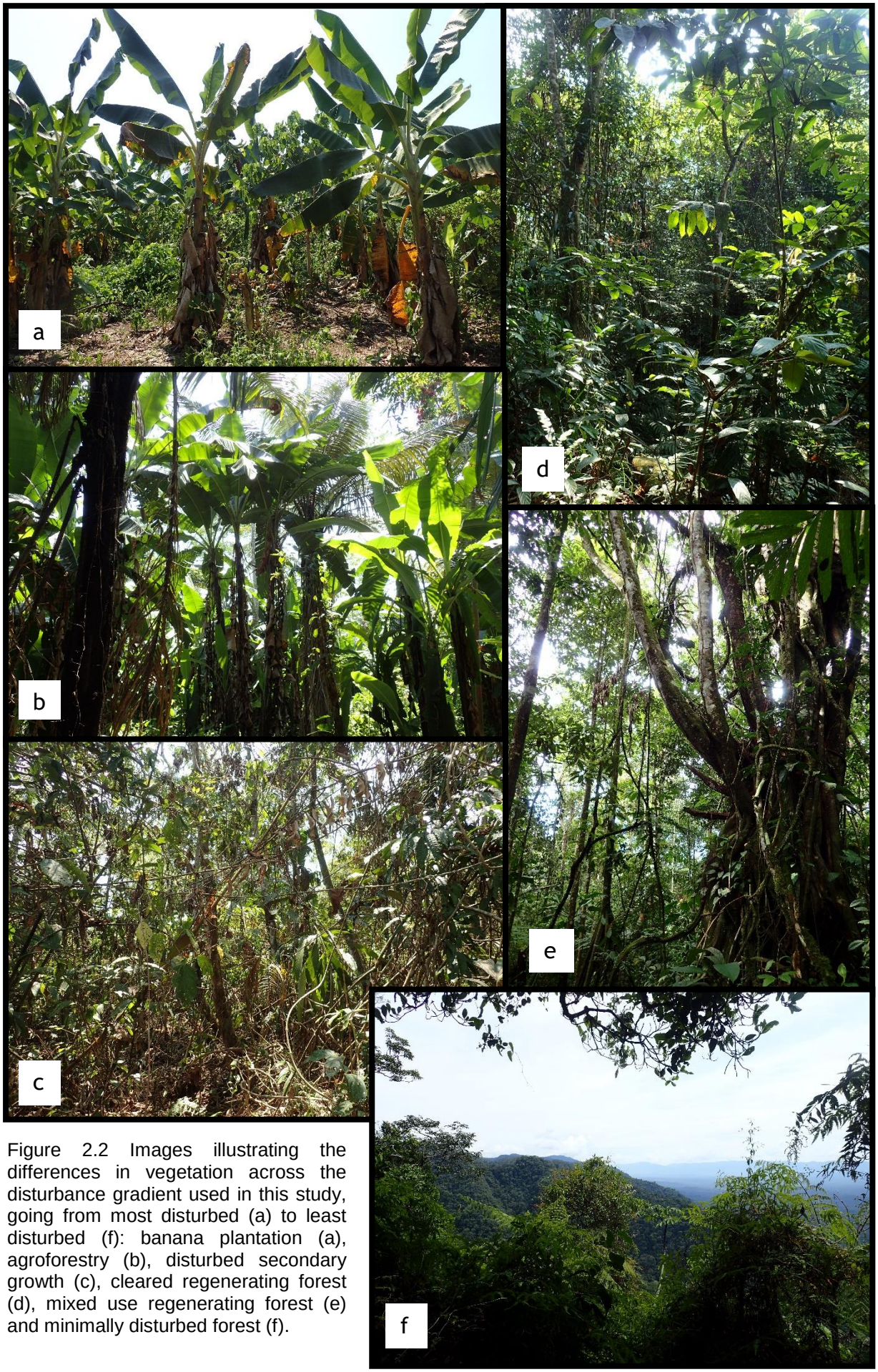

Figure 2.2 Images illustrating the differences in vegetation across the disturbance gradient used in this study, going from most disturbed (a) to least disturbed (f): banana plantation (a), agroforestry (b), disturbed secondary growth (c), cleared regenerating forest (d), mixed use regenerating forest (e) and minimally disturbed forest (f).

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2.2 Data collection

The different land uses identified in the region were ranked according to the perceived intensity of disturbance, which was tested using vegetation structure data, described later. Eighteen sites were included in the study, and a stratified site selection approach was used to ensure sampling was not dominated by a single disturbance history, with three sites chosen within each of the six disturbance types identified along the gradient (Table 2.1). The least disturbed sites were contiguous with the surrounding forest, whereas the agricultural sites were limited in size by the boundary of the cultivated area. The smallest site, one of the banana plantations, was approximately 0.7 ha, but the rest were all over 1 ha and below 5 ha. Potentially confounding effects of large landscape and climatic differences were minimised by selecting sites within a small geographic area (20 km^2), while ensuring sites of the same disturbance types were far enough apart (>500m) to avoid pseudo-replication of sampling. Sites of the different disturbance types were interspersed as much as possible (Figure 2.3), and kept close together to minimise spatial effects, given other constraints such as access and the locations of available sites.

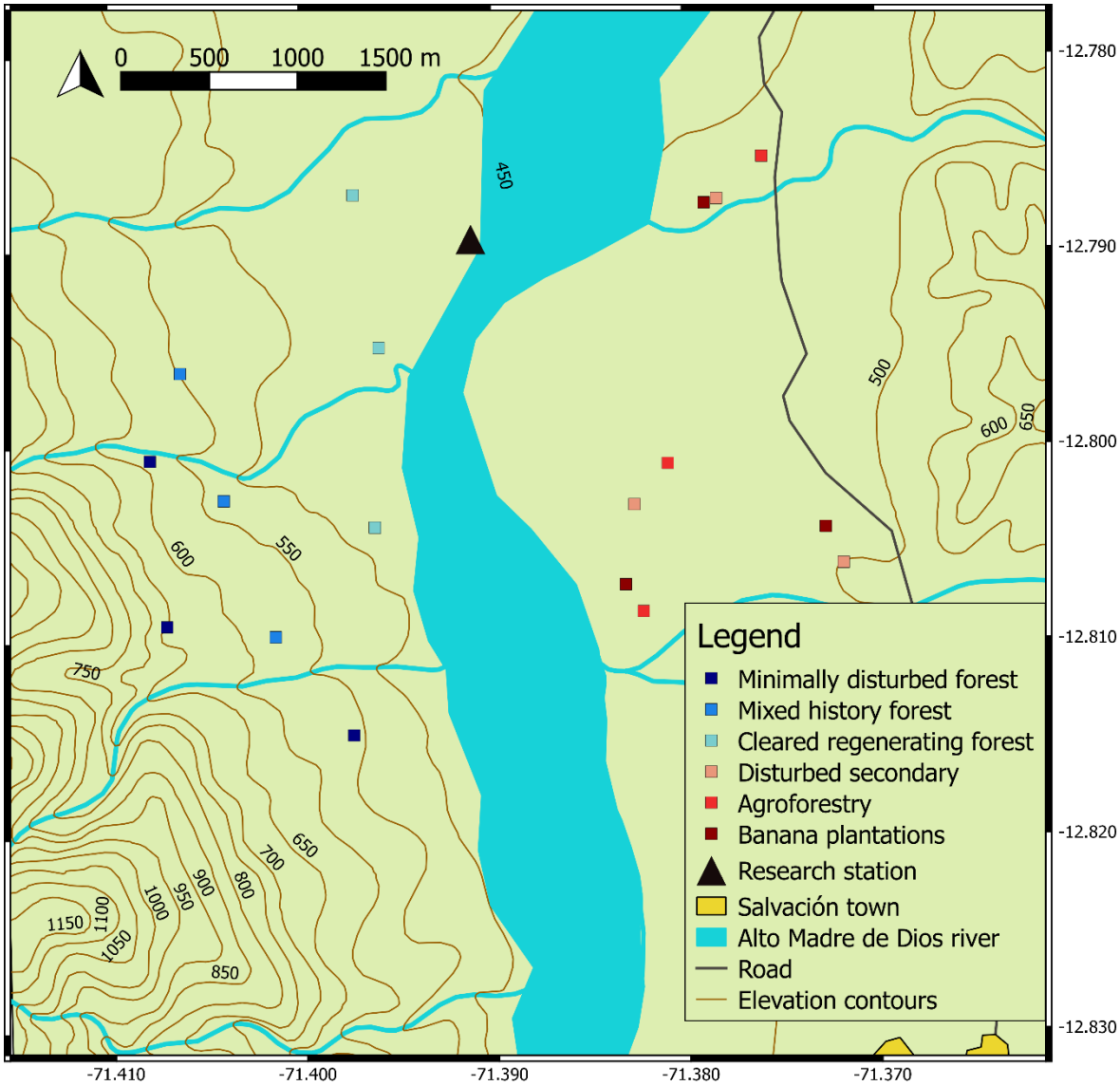

Figure 2.3 Map of study area. The map shows the eighteen study sites that represent the disturbance gradient, with their disturbance ranking indicated in the map legend. Intensity of disturbance is represented by a colour gradient, going from dark red (most disturbed) to dark blue (least disturbed). Contour lines represent elevation changes of 50m. The more disturbed and less disturbed sites are divided by the Alto Madre de Dios River, with a higher human population density east of the river.

Weather data were collected at the research station, with temperature, rainfall and humidity measured daily at 7am. Elevation data for each site was measured using Garmin GPS devices and Google Earth Pro, and distance to the main river, the Alto Madre de Dios, was measured in QGIS 2.18.7 (QGIS Development Team 2017), measuring the straight line distance from the centre of each site to the nearest edge of the river.

Table 2.1 Disturbance ranking and habitat descriptions

Rank	Habitat type	Description
1	Banana	Primarily banana monocultures (*Musa* spp.), but occasionally including a few other crop plants such as yucca (*Manihot esculenta*) or *Citrus*. Very open habitat with low vegetation.
2	Agroforestry	Banana plantations interspersed with native tree species, providing more shade and habitat complexity
3	Disturbed secondary	Uncultivated but heavily disturbed forest lying in between plantations, with more canopy cover and thick understorey vegetation
4	Cleared regenerating	Cleared regenerating forest — forest once cleared for agriculture and grazing, but regenerating under protection for over 30 years (according to the historical records of the Crees Foundation, unpublished), to form a closed canopy but with thick understorey vegetation
5	Mixed history	Selectively logged forest with small patches cleared for small scale cultivation but regenerating under protection for over 30 years – the canopy is well defined and the understorey less dense than rank 4, but large trees are scarce.
6	Minimally disturbed	Protected for over 30 years, with little evidence of previous disturbance — the canopy is high and well defined, large trees are present and the understorey is open.

The vegetation of each study site was assessed by selecting three random locations within the site (spinning the recorder around and throwing a ruler),

where a 25m^2 plot was marked out for vegetation sampling (results in Table S2.1). Within each plot, the following vegetation variables were measured: upper-canopy height, upper-canopy cover, mid-canopy height, mid-canopy cover, leaf litter depth, shrub and herb density around the plot, frequency of herbs, bare ground and course woody debris within the plot, number of trees with a diameter at breast height of >5cm, and the diameter of the three largest trees. Canopy height was estimated by an individual who had been previously trained using trees of known heights verified with a clinometer (the clinometer was not available for the full study), and these estimates were checked by a second trained member of the team. The same person conducted the vegetation measurements at all sites across the gradient to reduce observer bias in the estimates. Canopy cover was quantified using a quadrat held above the sampler's head and the quadrat used to estimate the percentage of canopy cover at five points within the plot (centre and corners). Understorey vegetation density was estimated at the four corners of the sampling plot using the modified Braun-Blanquet scale as described in Hurst and Allen (2007). I counted the number of trees with a diameter >5cm at breast height and measured the diameters of the three largest trees within each vegetation plot. Leaf litter depth was measured at 16 random points within the plot, and at each of these points I also recorded whether the ruler used to measure leaf litter also touched any herbs, bare ground or course woody debris. These followed the protocols for vegetation assessment used by Whitworth et al., (2016).

2.3 Analysis

The vegetation data were collated, and the mean values of the variables calculated for each plot within each site, since some variables comprised multiple measurements. These data were then fed into a Principal Component Analysis (PCA) to see which were most influential for separating the sites and to compare the sites of the different disturbance types.

Ranking the disturbance gradient based on land use is an approach that has been used in previous studies (Beck *et al*. 2002; Eggleton *et al*. 2002). However, in order to check if this ranking was appropriate, a Spearman rank correlation test was used to test the relationship between the disturbance rank of the sites and the differences in vegetations structure captured by the first axis of the PCA.

Since disturbance is largely determined by the presence of a human population and access via towns and roads, the more disturbed sites were clustered on the east side of the river, whereas the less disturbed forest was on the west, where a lack of roads and fewer human settlements reduced the pressure. It was not possible to fully control for these effects in the sampling design, but an attempt was made to reduce spatial correlation by interspersing the habitats as much as possible, and then the model residuals were tested for spatial autocorrelation in the analyses to check that this did not have a significant effect on the observed biodiversity patterns.

2.4 Results

The results of the PCA indicated that canopy height, canopy cover, number of trees, shrub and herb density and leaf litter depth were the most influential variables in separating the sites (Figure 2.4), and the less disturbed sites tended to be more positively associated with canopy height, canopy cover, number of trees, shrub and herb density, and negatively associated with leaf litter depth. The correlation test indicated a strong correlation between the vegetation structure and the disturbance ranking (rho = 0.91, $p < 0.001$; Figure 2.5).

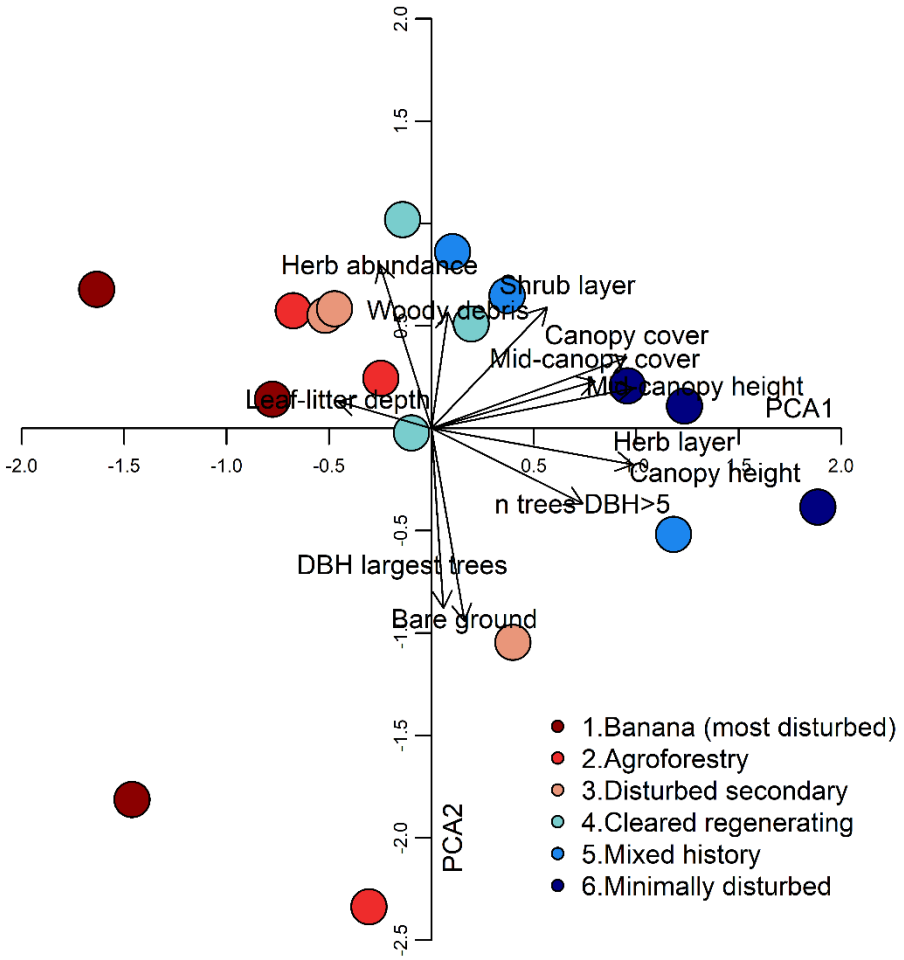

Figure 2.4 Vegetation PCA separating the sites based on the measures of vegetation structure. The circles represent the 18 study sites and the colours indicate the level of disturbance: dark red = most disturbed, dark blue = least disturbed.

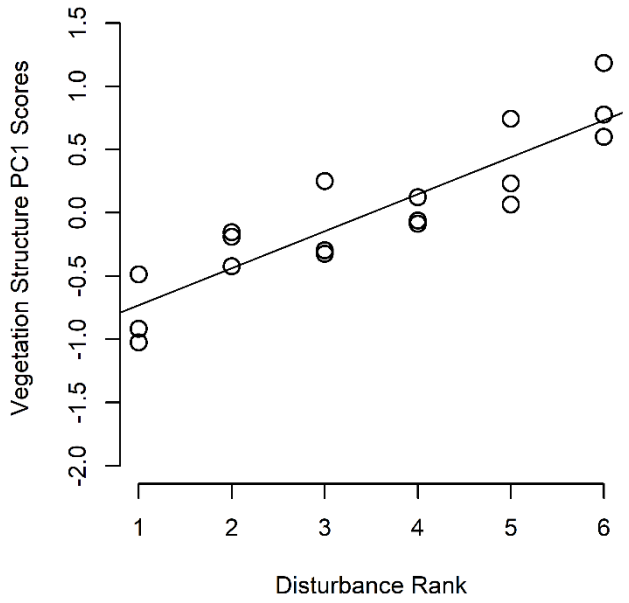

Figure 2.5 Correlation between vegetation structure and disturbance rank. Disturbance rank runs from the most disturbed (rank 1) to the least disturbed habitat (rank 6). The first axis of the principal component analysis of vegetation structure is positively correlated with canopy height, canopy cover and number of trees, and negatively with leaf litter depth.

2.5 Conclusion

The study area used in this investigation was typical of the land use patterns of the region. This meant that it was well suited for studying the effects of this type of disturbance on biodiversity, but also presented several challenges to data analysis, such as the more disturbed sites being generally closer to access routes and human habitation (Figure 2.3). Quantifying the intensity of disturbance was another difficulty, since it was important to recognise that there was a gradient going from lower to higher disturbance, but this could be approached in several ways. In this case, the decision was taken to rank the intensity of disturbance, and this made efficient use of the limited data available from 18 sites and was supported by the vegetation structure data. In order to overcome some of the limitations of this ranking approach, Spearman rank correlation tests were used throughout the analyses to test how each aspect of biodiversity changed along the disturbance gradient. This approach was feasible with the limited sample size available and made no assumptions about the shape of the relationship, including the relative size of the differences between disturbance levels or sites, only that the relationship was monotonic.

Linear models were then be used as an additional test to check if any patterns identified remained significant when controlling for other environmental variables, such as elevation and weather. Specific details of the analytical approaches are covered in the following chapters.

3 Dung beetles as indicators: what we measure matters.

3.1 Abstract

Most of the world's forests have undergone some degree of human disturbance, and this is only increasing. It is important to understand the impact that this disturbance has on biodiversity and ecosystem functions. Dung beetles (Coleoptera: Scarabaeidae) are sensitive indicators of the impacts of human disturbance. I aimed to identify which measures of diversity are most sensitive for identifying the response of dung beetles to disturbance, and to understand the impact of this disturbance on the ecosystem functions dung beetles provide.

I collected dung beetles from across a gradient of human disturbance in the Manu region of Peru. Multiple measures of alpha and beta diversity were measured and compared to assess dung beetle communities across the disturbance gradient. Alpha diversity was compared across the gradient using Hill numbers, with both observed and estimated diversity considered. Beta diversity was partitioned into the relative contribution of species nestedness and turnover, and changes in species composition evaluated. Dung removal experiments were undertaken to test whether ecosystem functions, specifically nutrient cycling and seed dispersal, differed across the gradient.

Dung beetle community composition changed across the disturbance gradient, with species preferring open habitats replacing forest specialists as disturbance increased. Alpha diversity decreased with increased disturbance when rare species were considered, but the number of dominant species showed no response. Two of the most important functional differences in dung beetles are body size and dung removal method — whether species are "rollers" or "tunnellers". Large species were more sensitive to disturbance than smaller ones, but I found no difference between rollers and tunnellers. Seed dispersal by dung beetles was negatively affected by increased disturbance. The information on dung beetle responses to disturbance gained from using multiple diversity measures could not be captured using any single measure alone. This study highlights the importance of considering multiple measures of diversity when

assessing the effect of forest disturbance, and the value of considering biodiversity patterns in the context of the wider ecosystem.

3.2 Introduction

The majority of the world's forests have been modified by human activity and are no longer classed as pristine (FAO 2015). The consequences of rainforest loss may be severe, with alteration of these ecosystems leading to a change in their constituent communities. This in turn affects the ability of these communities to provide essential functions and services (Hooper *et al*. 2005). The resilience of a forest depends on species that carry out functions such as pollination and seed-dispersal, and that are often lost during land conversion (Stork *et al*. 2009; Dent & Wright 2009).

As much of tropical forest is disturbed, it is important to assess the impact of distinct levels of disturbance to improve land management practices and monitor conservation efforts. Applying a gradient approach to ecological research on environmental disturbance has several benefits, including the potential to account for spatial variation in the environment, detect subtle changes in the community of interest, and to predict species responses to future disturbance or restoration (Chazdon *et al*. 2009). One might assume that high biodiversity is only sustainable at low levels of disturbance. However, large areas of disturbed forest can contribute to biodiversity conservation, especially if regeneration is permitted to occur (Dent & Wright 2009; Edwards *et al*. 2010; Struebig *et al*. 2013). Some types of agriculture and fallow vegetation can also support significant levels of biodiversity and provide valuable ecosystem services (Montagnini & Nair 2004; Montagnini *et al*. 2005; Peh *et al*. 2006; Barlow *et al*. 2007a). The heterogenous nature of degraded landscapes can provide many resources, although biodiversity is probably sustained best when these lie alongside areas of continuous forest (Peh *et al*. 2006). Quantifying the effect of disturbance on biodiversity requires the use of sensitive measures, and indicator taxa are a useful tool for assessing habitat quality (Brown 1997; Favila and Halffter 1997; Gardner et al. 2008).

Dung beetles are valuable biological indicators of the wider consequences of disturbance for biodiversity and ecosystem functions. They are efficient to

sample and taxonomically accessible (Favila & Halffter 1997; Gardner et al. 2008; Spector 2006), display graded responses to habitat modification (Gardner et al. 2008), are ecologically important (Favila & Halffter 1997; Spector 2006), globally distributed and correlate well with total biodiversity (Spector 2006). They also provide important ecosystem functions and services such as soil aeration, improved water penetration, nutrient sequestration into the soil (Beynon *et al.* 2012), control of fly and parasite populations (Grønvold, Sommer & Nansen 1992), seed dispersal and improved seed germination (Shepherd & Chapman 1998; Koike *et al.* 2012). These functions are at risk should we lose the dung beetles that provide them.

Many measures of diversity have been used to assess the response of dung beetles to human disturbance, with different patterns found depending on the disturbance type and the diversity metric used. The choice of metric used in biodiversity studies is an important one, as this can often affect the detection of relationships. Most biodiversity measures focus on species as the unit of interest, although phylogenetic and functional diversity may provide additional information on the responses of ecosystems to environmental change (Magurran 2004). Alpha diversity focuses on the presence and relative abundance of species at individual sites. Measures of alpha diversity include species richness, which considers all species as contributing equally to the diversity of a site, Berger-Parker diversity, which considers only the most dominant species, and Shannon and Simpson diversity, which place intermediate emphasis on rare species. Hill (1973) demonstrated that these fall along a continuum of possible diversity measures, from species richness to Berger-Parker. Beta diversity, measuring the changes across sites, includes many different measures that cover species turnover, nestedness of communities and similarity of community composition. Gamma diversity can be considered as the diversity of the overall region. It is desirable that the diversity measures used are mathematically consistent, allowing for easier comparison and more intuitive understanding of the differences between sites and studies (Chao *et al.* 2014; Hill 1973; Reeve *et al.* 2016).

Between site variation in alpha diversity is most often measured using species richness, but Shannon, Simpson and Fisher's alpha are also widely used. Dung beetle species richness and other alpha diversity measures are generally thought

to decline with increasing disturbance (Nichols *et al*. 2007; Davis & Philips 2009; Horgan 2009; Slade, Mann & Lewis 2011), but Hayes *et al*. (2009) found that detected patterns depend strongly on the metric of alpha diversity used. There are many measures of beta diversity, and their responses to disturbance are less often studied than alpha diversity measures, and can be sensitive to the spatial scale or sampling design used (Marsh & Ewers 2013). In some cases, high species turnover between disturbance categories has been found (Scheffler 2005; Nichols *et al*. 2007; Davis & Philips 2009), but in others turnover was low, with disturbed habitats containing a subset of the species found in less disturbed forest (Horgan 2009; Slade, Mann & Lewis 2011). Abundance of dung beetles declines in response to some types of forest disturbance (Nichols *et al*. 2007), including agricultural conversion, but can recover rapidly with habitat regeneration (Barnes *et al*. 2014). Beetle biomass decreases in response to disturbance in some cases (Horgan 2009), but in others a large number of small beetles can make up the biomass where larger species are lost (Scheffler 2005).

Vegetation structure is a strong driver of dung beetle habitat choice and, even when resources are available, many beetles will not cross ecotones (Klein 1989). Crops that provide forest cover, such as shade-coffee or arguably the banana-agroforestry plots found in Manu, can help maintain diversity by providing corridor and buffer habitats between forest fragments and around core protected areas fauna (Davis and Philips 2009; Harvey *et al*. 2006; Horgan 2009). In general, dung beetle species richness, community similarity to that of intact forest, abundance and evenness decline with increasing levels of habitat modification (Nichols et al. 2007; Table S3.1). Assemblages in agroforestry and tree plantations were usually intermediate between intact forest and open pastures (Nichols *et al*. 2007). Stork *et al*. (2017) emphasized the importance of considering the responses of different functional groups, and to different components of disturbance (e.g. loss of tree cover, soil compaction etc.). Measures of species composition, species diversity and functional diversity can complement each other and contribute to a better understanding of the efficacy of restoration practices (Audino, Louzada & Comita 2014). Choosing indices carefully with respect to their biological relevance is important and, where possible, it may be helpful to include several diversity measures to quantify the effects of disturbance (Hayes *et al*. 2009).

Not all dung beetles show the same responses to disturbance. Dung beetle communities can be split into functional groups based on diet, body size, activity period and method of dung removal and different functional groups may be more or less responsive to disturbance (Nichols *et al*. 2013). Dung beetles are classified as rollers (telecoprid), if they form a ball from the dung and roll this away from the deposit before burying it, or tunnellers (paracoprid), who dig directly under the dung to bury it. Some species tunnel into the dung but don't bury it and are classed as dwellers (endocoprid) (Hanski & Camberfort 1991). In cases where the responses of functional groups have been examined separately, contrasting responses have been found. Richness of roller species declined with increased disturbance in some studies, while tunnellers show no response (Vulinec 2002; Hayes *et al*. 2009). Beetles of different sizes may also respond differently, with large beetles appearing to be more sensitive to forest loss than smaller species (Horgan 2008; Barragán *et al*. 2011).

Ecosystem functioning depends on biomass, abundance and specific functional groups of dung beetles. Species richness has been suggested to correlate positively with dung removal and decomposition (Slade, Mann & Lewis 2011; Beynon *et al*. 2012). A high biomass of beetles is valuable for dung decomposition but functional richness of the assemblage present is also important (Horgan 2005; Nichols *et al*. 2009; Braga *et al*. 2013). Some functional groups have been found to have a greater impact on ecosystem functions than others: large beetles, for example, have been found to contribute disproportionately to seed dispersal and dung removal (Slade *et al*. 2007; Braga *et al*. 2013). However, for maximum functioning, a full complement of functional groups is necessary, as there is evidence of overyielding among functional groups and complex interactions between species (Slade *et al*. 2007; O'Hea, Kirwan & Finn 2010; Manning *et al*. 2016). The conservation of functional richness is therefore important to maximise the ecological functions and services provided by dung beetles (Nichols *et al*. 2008).

I studied dung beetle diversity across a disturbance gradient in the Manu Biosphere Reserve in Peru, a country that has lost over 3,780,400 ha of forest cover due to land conversions since 1990 (FAO, 2010; 2017). Previous studies have mostly focused on how dung beetles are affected by human disturbance (Table S3.1). In this study, I aim to identify which measures of dung beetle

diversity are most useful as indicators of the impacts of disturbance. Dung beetles are widely used as ecological indicators, however their responses to disturbance have been quantified using a wide variety of measures and there is not enough evidence as to which are the best measures to use for this taxonomic group. I also explore whether some of the ecosystem functions provided by dung beetles are affected by human disturbance. I compare multiple alpha and beta diversity measures and some simple functional measures across a disturbance gradient in human impacted tropical forest. I hypothesised that:
dung beetles decline in alpha diversity in more disturbed sites, with rarer species more sensitive than dominant species; there is a change in the species composition of dung beetles across the disturbance gradient; there is a decrease in the overall abundance of dung beetles in more disturbed sites and there is a reduction in the ecosystem functions performed by dung beetles in more disturbed sites, which could be detected by lower rates of seed dispersal, dung removal and soil nutrient levels.

3.3 Methods

3.3.1 Study area

Research was conducted in and around the Manu Learning Centre (UTM Zone 19L 240350 E, 8584900 S, 470 m above sea level) in the cultural zone of the Manu Biosphere Reserve in southeast Peru (Figure 2.1), one of the most biodiverse places on earth (Patterson, Stotz & Solari 2006; Catenazzi, Lehr & Von May 2013). This area of lowland tropical forest, in the foothills of the Andes, acts as a buffer to the core of Manu National Park. It is subject to low-level protection but human activities including subsistence agriculture and logging are permitted, as well as ecotourism activities. This has created a matrix of habitats of different disturbance intensities, including areas of high quality forest as well as farmland, logged forest, plantations and areas of regenerating forest, and is typical of forest conversion patterns found in many parts of the tropics (Struebig *et al.* 2013). Details of the 18 study sites used to represent this disturbance gradient are presented in Chapter 2.

3.3.2 Data Collection

3.3.2.1 Dung beetle diversity

Four pitfall traps were placed in each site at 50 m intervals, following standard dung beetle survey methodologies (Larsen & Forsyth 2005), including maintaining >30m between the pitfall traps and the site boundary. This trap spacing was not possible with four traps in the smallest site, so two pitfalls were run for twice the time. Traps were baited with *c.*25 ml human faeces, checked every 24 hours, rebaited every 48 hours and left open continuously for five days at each site. Data from all trap-days were pooled for analysis. All captured beetles were preserved in 70% ethanol and later identified using the reference collection at the Museo de Historia Natural de Cusco and relevant literature (Edmonds & Zidek 2004, 2010, 2012; Génier 1996; Genier 2009; Larsen, Génier & Sthapit 2008; Ocampo 2006; Valencia *et al*. 2016; Vaz-De-Mello *et al*. 2011).

3.3.2.2 Ecosystem functions

To quantify the ecosystem functions performed by dung beetles, a field experiment was set up to investigate dung removal and seed dispersal in response to human disturbance. The experimental design was closely based on Braga *et al*. (2013) and involved placing a 100g ball of swine dung in the centre of an arena, covered with a small plastic plate on stilts to reduce weather impacts, and with a low fence preventing removal of dung beyond its 70cm radius. Spherical beads representing seeds of three sizes (50 small beads: 3 mm diameter, glass; 20 medium beads: 8 mm diameter, wood; 10 large beads: 17 mm diameter, wood) were mixed into the dung ball, and the arena was then left for 24 hours. The following day, the amount of dung remaining in the central pile was weighed and the number of beads dispersed were counted. Different combinations of two habitat types (one site of rank 1-3 and one of rank 4-6) were sampled simultaneously to control for the effect of weather. Two arenas were set up at each site, and each site was sampled for two 24 hr periods (n = 4 per site) between May and July 2016. Soil samples were taken from each site following the protocol of the Food and Agriculture Organisation of the United Nations (Villasanti, Román & Pantoja 2013) and were sent to the laboratory of the faculty of agronomy at the Universidad de La Molina, Lima, Peru, to quantify potassium, phosphorus and organic matter content.

3.3.3 Analysis

3.3.3.1 Dung beetle diversity calculation

Dung beetle alpha diversity was calculated for each site using Hill numbers; these consist of a continuum of diversity measures along different viewpoint parameters, q, with decreasing emphasis on rare species as the value of q increases (Hill 1973; Reeve *et al*. 2016). I calculated diversity at q = 0, 1, 2 and ∞, as these are equivalent to the following commonly used diversity measures: species richness, Shannon entropy, Simpson diversity and Berger Parker diversity, so can be easily compared to previous studies. The raw diversity values were calculated using the package rdiversity (Mitchell & Reeve 2016) in R version 3.3.2 (R Core Team 2017). Estimates of diversity for each of these values of q were also calculated using the package iNEXT version 2.0.14 (Chao *et al*. 2014; Hsieh, Ma & Chao 2016) to rarefy and extrapolate the data to compare sites at equal sampling coverage. For q = 0, extrapolation beyond double the sample size is advised against (Hsieh, Ma & Chao 2016), so the sites were compared at a sample size of 300 individuals, which was close to 95% sampling completeness for all sites (Figure 3.1), and the same was done for diversity q = 1 and q = 2, with the estimates bootstrapped 100 times.

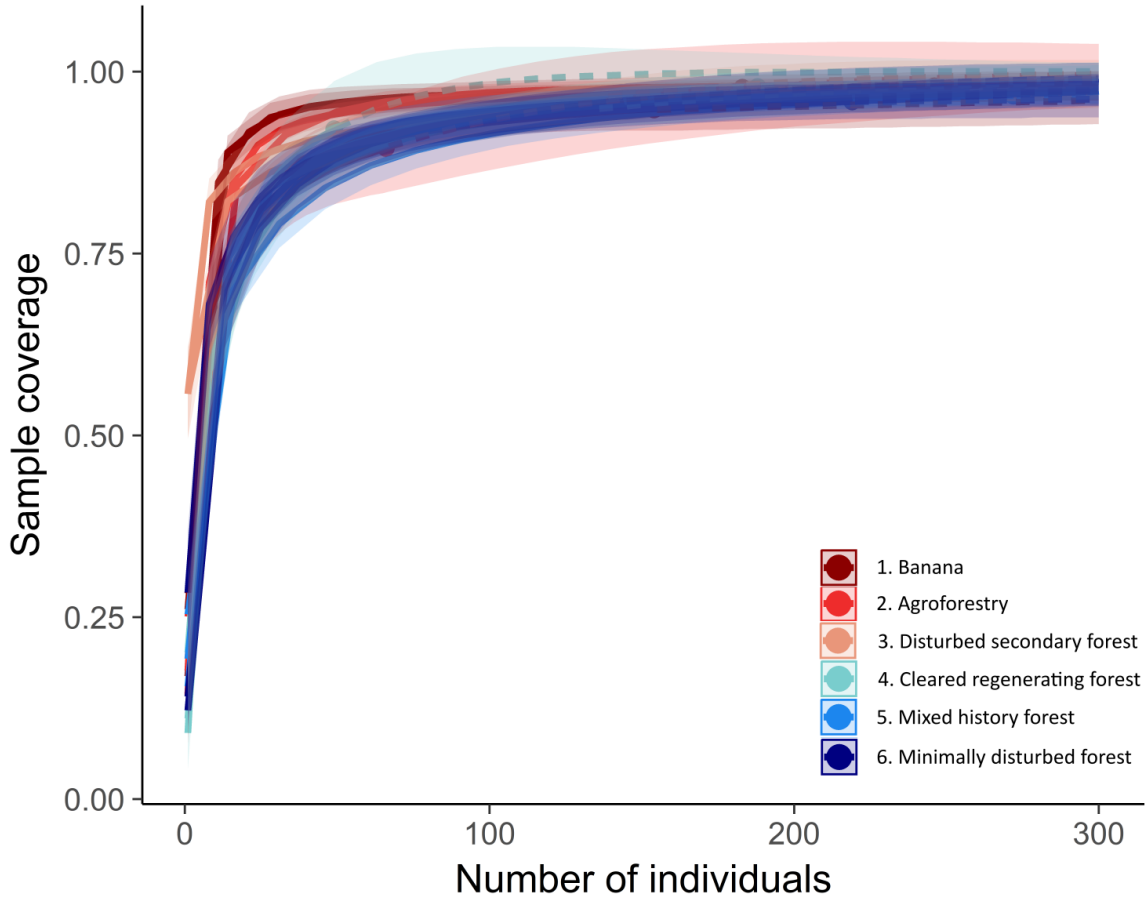

Figure 3.1 Sample coverage of all sites. Confidence interval for rarefaction/extrapolation estimates generated using the iNEXT package in R. All sites have reached close to or over 95% sample completeness at a sample size of 300 individuals. Sites are colour coded from most disturbed (dark red) to least disturbed (dark blue), and the transition from a solid line to a dashed line is where the estimate changes from rarefaction to extrapolation.

For each value of q, the raw estimates were extracted from the iNEXT bootstrapping results (1000 runs), and the proportion of cases where the diversity of the less disturbed habitat was higher than the more disturbed habitat was calculated for all pairs of habitats. It was feasible to run more bootstraps to calculate the raw estimates, as this was less computationally intensive than running the full iNEXT function. The proportion of times the less disturbed habitat was more diverse was tested for correlation with the difference in the habitat disturbance levels using a Spearman rank correlation test (Spearman 1904). This approach enabled me to assess the significance of the pattern shown by the mean diversity estimates while accounting for the uncertainty in the diversity estimates.

3.3.3.2 Diversity and ecosystem function statistics

Dung beetle species were classified into functional groups based on body size and dung removal behaviour, according to information available in published literature (Barragán *et al*. 2011; Braga *et al*. 2013; Damborsky *et al*. 2015; Daniel *et al*. 2014; Figueroa and Alvarado, 2011; Gardner *et al*. 2008; Génier 2009; Griffiths *et al*. 2016; Horgan 2009; Larsen *et al*. 2008, 2006; Rendón and Uribe 2010). I focused on the differences between small and large beetles, and between rollers and tunnellers, as the relative contributions of these groups have been shown to influence ecosystem functioning (Braga *et al*. 2013). There were very few dwellers collected, so these were combined with tunnellers, since they do not contribute towards horizontal seed movement like rollers. Mean body length (12.7 mm) was used as the threshold between 'small' and 'large' beetles; this threshold matched a subjective division by volunteers who were asked to divide beetles into size categories for another experiment (unpublished). Abundance and alpha diversity of these groups were calculated separately and compared across the gradient.

I used Spearman rank correlation tests to examine relationships between disturbance and diversity or function. I used this approach as it assumes neither a normal distribution or a linear relationship between the variables, only that the relationship is monotonic. As there were multiple measures from each disturbance rank, the data were randomly resampled to provide a confidence interval for the correlation coefficient, overcoming the issue of data ties in the correlation test. Throughout the results section, the statistics reported are the results of the Spearman rank correlation test unless stated otherwise (full results in Tables S3.3). In the case of the observed alpha diversity results, the correlation between alpha diversity and disturbance was tested at each value of q individually, but to identify if there was also a significant response of overall alpha diversity, a permutation test was used to calculate the combined p value of the correlation between alpha diversity at $q = 0, 0.5, 1, 2$ and ∞ and disturbance rank.

Where a significant correlation was identified, linear models were then used to control for the effect of other environmental variables (distance to river, elevation and weather). Linear models with a Gaussian distribution and a logged

response were used to test the effect of disturbance on diversity and abundance (of the whole community and the separate functional groups), soil macronutrient levels (organic matter, phosphorus and potassium), controlling for the environmental variables listed above. Stepwise selection was used to test if any of the environmental variables resulted in a significant improvement in the model (Table S3.4), in which case they would be retained (best fitting models presented in Table S3.5). Linear mixed models with random effects for date and arena nested in site were used to test the levels of dung removal and proportion of beads dispersed in response to disturbance. Dung removal was modelled using a Gaussian distribution and logged response, whereas for the proportion of beads dispersed I used a binomial distribution with an added observation level random effect included to correct for overdispersion. Model selection was carried out using likelihood ratio tests (Tables S3.4 and S3.5). The residuals of the models were tested for spatial autocorrelation using Moran's I (Table S3.6).

To avoid collinearity issues, I excluded some measured variables from the models. There was little variation in humidity and temperature across the survey period, and these were controlled for in the study design. Rainfall was collinear with temperature and humidity but showed much more variation across the survey period, so was included in the linear models as an additional control. Distance to roads was strongly correlated with disturbance rank but, as it could also be considered a measure of human disturbance, it was not included in the models.

The community composition (species present and relative abundances) of the sites were compared using a redundancy analysis (RDA) constrained by disturbance rank, distance to the river and elevation, using the vegan package in R (Oksanen *et al*. 2018). A Hellinger transformation of the species x site matrix was used for the redundancy analysis, in order to minimise the influence of very rare species as well as large differences in species abundances between sites (Legendre & Gallagher 2001). Beta diversity was partitioned into a change in richness and a turnover of species across the gradient to see which contributed more to beta diversity, using the quantitative form of the Sorensen family of coefficients to obtain the percentage difference index (Legendre 2014; Dray *et al*. 2017) using the package adepatial (Dray *et al*. 2018). The species that varied most in their abundance across the gradient were identified using the Species

1291 Contribution to Beta Diversity (SCBD) index, also in adespatial (Legendre & De
1292 Cáceres 2013; Legendre & Gauthier 2014).

1293

3.4 Results

3.4.1 Alpha diversity

A total of 3,787 individuals of 57 species (Table S3.2) were collected over a three-week period in August 2015. Of these 57 species, five were only detected once, and four were detected twice during the course of the study. Alpha diversity overall decreased significantly with increased disturbance intensity (Figure 3.2), for observed and estimated diversity (permuted combined p value of correlation of observed alpha diversity at q = 0, 0.5, 1, 2 and ∞ with disturbance, p = 0.008); estimated diversities at q = 0, 0.5, 1 and 2 at a sample size of 300, permuted combined p value of correlation with disturbance: p = 0.02). However, this pattern was mostly a result of a strong correlation between disturbance and species richness (q = 0) and Shannon diversity (q = 1). At q = 0, higher disturbance resulted in lower observed (rho = 0.73, p < 0.001) and estimated species richness (rho = 0.59, p = 0.01), and lower observed diversity at q = 1 (rho = 0.51, p = 0.03). At higher orders of q, there was no effect of disturbance on diversity, with similar numbers of more dominant species being found at all disturbance levels (Figure 3.2). This indicates that although there are more species present in less disturbed environments, their distribution is uneven. There was no significant change in total beetle abundance across the gradient (rho = -0.02, p = 0.88).

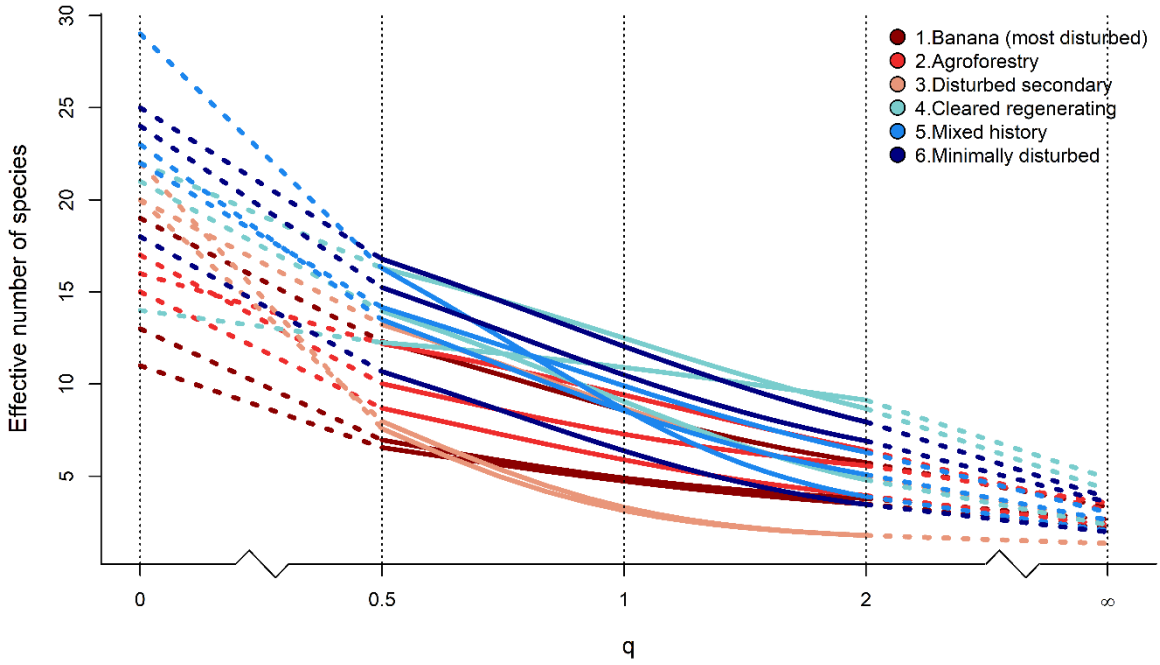

Figure 3.2 Alpha diversity of dung beetles across a human disturbance gradient. The viewpoint parameter at which diversity is calculated is represented by 'q'. At q = 0, all species are equally weighted; at higher values of q, dominant species count more. Alpha diversity is represented as the effective number of species present at each site. The disturbance intensity of each site is represented by a colour gradient ranging from dark red (most disturbed) to dark blue (least disturbed).

For estimated diversity at q = 0 the difference in diversity between a pair of sites correlated strongly with the difference in disturbance levels even when uncertainty in the diversity estimates was accounted for by resampling (rho = 0.76, p = 0.001; Figure 3.3). No such correlation was apparent at q = 1 or 2 (Figure 3.3).

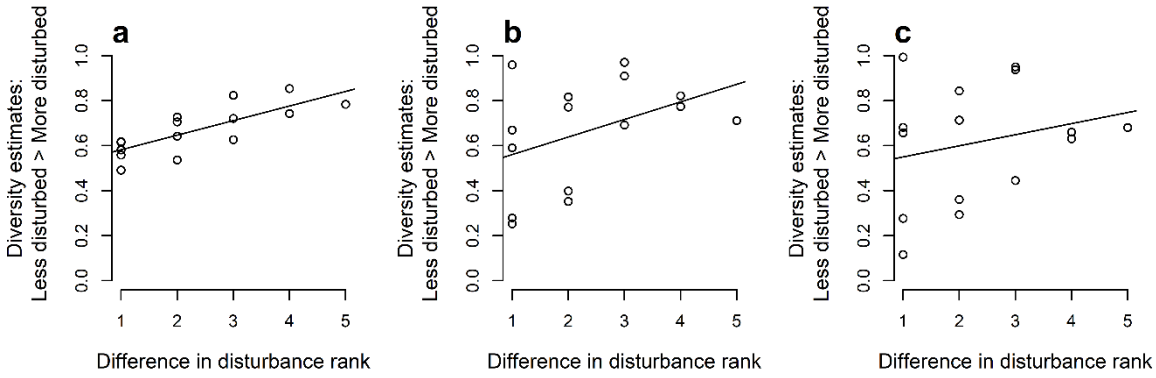

Figure 3.3 Correlation between diversity estimates and disturbance ranking. The proportion of times that the less disturbed habitat was estimated to have a higher diversity than the more disturbed habitat is based on 1000 estimates calculated using the iNEXT package in R, comparing all possible habitat pairs. This is plotted against the difference in disturbance rank between the pairs of habitats (higher values mean the sites are further apart along the gradient). Figure 3.3a shows the relationship at q = 0, 3.3b at q = 1 and 3.3c at q = 2.

3.4.2 Functional groups

Observed diversity of both rollers and tunnellers decreased with increasing disturbance. This pattern was apparent at all orders of q for rollers, and for all except q = ∞ for tunnellers, with the strongest correlations at lower q values (rollers at q = 0: rho = 0.60, p = 0.008, tunnellers at q = 0: rho=0.69, p = 0.001). Visual examination of abundance across the gradient suggested slightly higher numbers of rollers in more disturbed areas, and the reverse trend for tunnellers (Figure S3.3). However, there was no statistically significant correlation between disturbance rank and the abundance of rollers (rho = -0.25, p = 0.32) or tunnellers (rho = 0.24, p = 0.34).

There was no change in diversity or abundance of small beetles across the disturbance gradient. Observed species richness and Shannon diversity of large beetles declined with increased disturbance (q = 0: rho = 0.83, p < 0.001; q = 1: rho = 0.61, p = 0.008), and this trend was apparent at higher q values but not statistically significant.

3.4.3 Beta diversity

There was a clear difference in dung beetle species composition across the gradient (Figure 3.4), with 39% of the variation explained by the first component of the redundancy analysis (RDA1). This is driven by a change in the species present as well as their relative abundances. When partitioned, 14% of the beta

diversity was found to be due to a change in species richness (nestedness), and 86% due to replacement of species along the gradient (turnover). The alpha diversity results (Figure 3.2) demonstrated a significant change in species richness across the gradient. However, it seems that whilst there is a loss of species with increased disturbance, even more notable is the turnover of species found across the gradient, meaning that the nestedness of the sites is low.

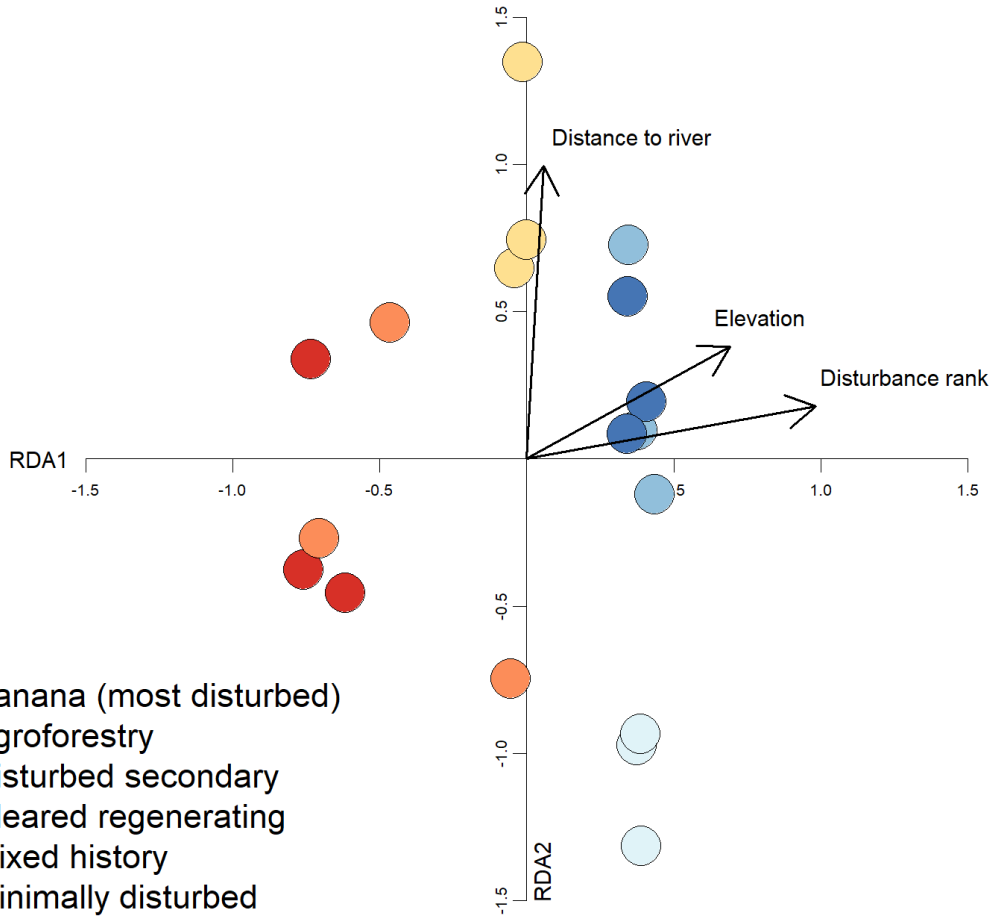

Figure 3.4 Dung beetle community composition redundancy analysis. The x and y axes represent the first two axes of the redundancy analysis of community composition, considering species present and their relative abundances across the gradient and constrained by disturbance rank, elevation and distance to the river. The colours of the points represent the gradient of disturbance; red represents the most disturbed habitat, and dark blue the least disturbed.

The species that varied most across the gradient were evident from the SCBD index (species contributions to beta diversity), and the abundances of the ten most influential species were compared across the gradient. *Canthon virens* Mannerheim, 1829, *Canthon monilifer* Blanchard, 1846 and *Eurysternus nigrovirens* Génier, 2009 were found almost exclusively in the most disturbed habitat types, whereas *Onthophagus rubrescens* Blanchard, 1843 and *Eurysternus*

hypocrita Balthasar, 1939 showed a preference for the less disturbed habitats (Figure 3.5).

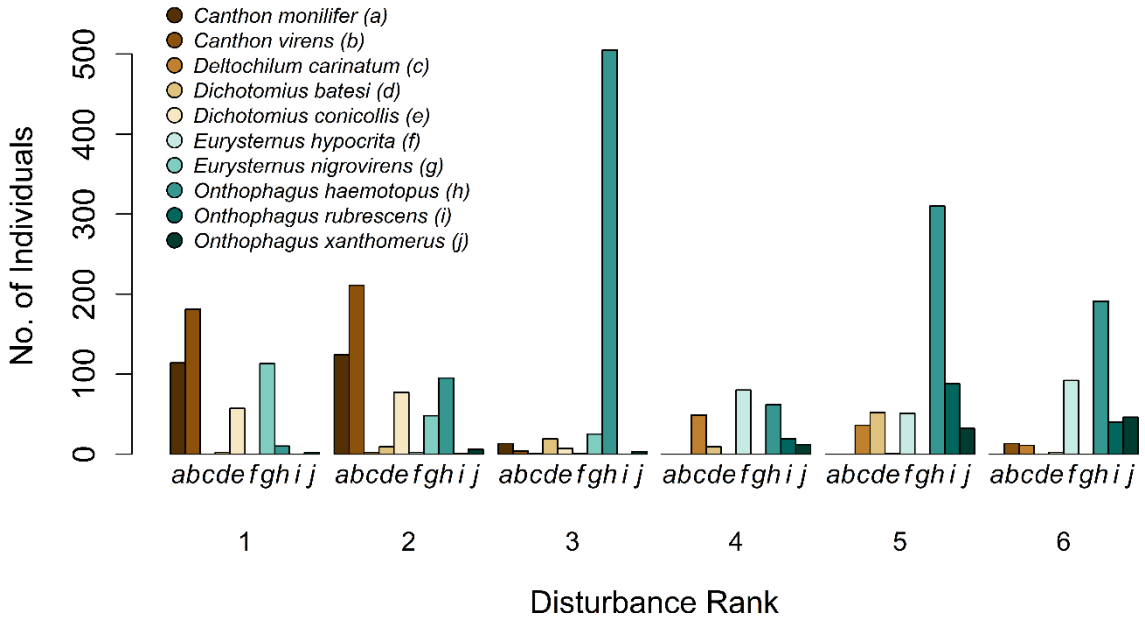

Figure 3.5 Species contributions to beta diversity and changes in abundance. Total abundances of the ten species with the highest Species Contribution to Beta Diversity scores at the six disturbance levels, indicating the habitat preferences of the species.

3.4.4 Ecosystem functions

No significant effect of disturbance on dung removal or soil nutrient levels (organic matter, phosphorus and potassium) was identified (Figure S3.1 and Figure S3.2). There was an overall decrease in dispersal of the artificial seeds as disturbance increased (Fisher's combined probability with six degrees of freedom (Fisher 1925); $X^2 = 18.39$, $p < 0.001$). When the different sizes of beads were considered there was a decrease in the proportion of small and medium beads dispersed as disturbance increased, but not for large seeds (small seeds: $p = 0.04$, rho = 0.24; medium seeds: $p = 0.01$, rho = 0.30; large seeds: $p = 0.24$, rho = 0.14; Figure S3.1).

3.5 Discussion

Human disturbance is linked to changes in the diversity of dung beetles that could result in a loss of ecosystem functions in disturbed areas, reducing soil fertility and seedling establishment. I found that dung beetle alpha diversity

decreased with increased human disturbance. Beta diversity across the gradient was primarily due to a turnover of species, with forest specialists giving way to species with a preference for more open habitats. Large species showed a stronger negative response to disturbance than smaller ones and are thought to contribute more to ecosystem functioning (Nervo *et al*. 2014). I found evidence for a reduction in secondary seed dispersal (much of the primary seed dispersal is conducted by fruit and plant-eating mammals and birds, and dung beetles then further disperse the seeds deposited in mammal dung) as disturbance increased across the gradient.

The change in alpha diversity of dung beetle communities across the disturbance gradient was mostly driven by a change in the number of rare species present, with similar numbers of dominant species found throughout the gradient (Figure 3.2). This corroborates the findings of most studies of dung beetle species richness in relation to human disturbance (Table S3.1). Rare species found in forests may be more highly specialised for forest habitats, either because of the mammal species present or the physical attributes of that habitat type, such as humidity, soil type and shade. Therefore, where alpha diversity is used to detect changes in communities due to disturbance, low q values are likely to provide the most sensitive measures. However, one of the challenges in this is that many species were only detected once or twice, whereas others were recorded in their hundreds. The species accumulation curves suggested that the sampling effort was sufficient despite this, and I chose not to exclude the singletons and doubletons because I was interested in how these rare species would influence the comparison of the different diversity measures, since they would be highly weighted at $q = 0$ but have very little contribution at values of $q > 0$.

Rollers and tunnellers both responded negatively to disturbance, with observed diversity declining with increased disturbance for both groups and a slightly stronger response seen for tunnellers. Most previous studies found that rollers were the more sensitive group (Table S3.1). However Barragán *et al*. (2011) found large, nocturnal tunnelers to be more sensitive to habitat conversion than other functional groups. I found large beetles to be more sensitive to disturbance than small beetles, supporting the findings of previous work (Table S3.1). The decline of large species was apparent even at higher orders of q, indicating that both rare and common species were lost as disturbance

increased. Large beetles are likely to require more dung resources and there may be insufficient dung available to sustain these larger species if populations of large mammals are reduced in the more disturbed areas, whereas smaller dung beetles may be able to sustain themselves on the dung of smaller, more abundant mammal species. Large beetles have been identified as having a greater impact on ecosystem functions than smaller species, so their loss is of particular concern (Larsen, Williams & Kremen 2005; Slade *et al*. 2007). Within the less disturbed sites (ranks 4-6), previous research found no difference in the abundance or richness of medium-large mammals between the disturbance categories (Whitworth 2016), but a difference in the mammal population may have been more apparent had data been available across the full gradient.

My study supports the findings of previous work that dung beetles are a useful indicator group, as they are sensitive to human disturbance and can be easily sampled. However, whilst dung beetle species richness and Shannon diversity are useful measures for detecting the effects of disturbance, changes in dung beetle community composition are more sensitive and functional diversity should also be considered, as recommended for other taxa (Stork *et al*. 2017). Several previous studies in the region have identified this as an area of high dung beetle richness and reaffirmed the value of dung beetles as indicators (Valencia 2001, 2014; Valencia *et al*. 2009) and, at the location of this study, dung beetle abundance was found to be a good predictor of habitat disturbance (Valencia *et al*. 2004), although I found no correlation between dung beetle abundance and human disturbance in this study. One of the caveats of this study was that it was designed so that the distance between sites was not a limiting factor to the distribution of species across the area, making it easier to relate any differences in biodiversity metrics to differences in the land use as opposed to other environmental differences present at larger scales. However, this does mean that it was possible for mobile species, such as dung beetles, to move between sites to some extent, which has the potential to dilute our power of detecting any differences between the sites and increase the risk of a type II error. Whilst this does reduce our confidence in the results where we detected no difference across the gradient, it lends greater weight to those significant differences that were detected.

For dung beetle assemblages, species richness and abundance have been found to be poor predictors of ecosystem functioning, whereas Shannon diversity and evenness, and trait-based and functional diversity indices, have been more effective (Gagic *et al*. 2015). Community composition is of particular importance for optimal ecosystem functioning (Larsen, Williams & Kremen 2005). Community similarity can be more effective than species richness for identifying cross-taxon congruency in responses (Su *et al*. 2004). Stork *et al*. (2017) found that community composition was more sensitive to disturbance than species richness for several taxonomic groups.

Change in the dung beetle community across the disturbance gradient was primarily due to a turnover of species, an important point that is overlooked when only alpha diversity is considered. Not only was there a loss in the number of species, but there was a shift from domination by forest specialists to open habitat and agricultural species as disturbance increased (Figure 3.4). I found a strong preference of three species for more disturbed habitats: the endocoprid *Eurysternus nigrovirens,* and two rollers considered indicators of deforestation, *Canthon monilifer* and *Canthon virens*, preferring agricultural areas (especially agroforestry), and cerrado and other open habitats respectively (Génier 2009; Horgan 2009). In most pristine habitats, I found *Eurysternus hypocrita*, a large endocoprid species that prefers primary forest (Génier 2009; Braga *et al*. 2013); I found it in regenerating forest (disturbance ranks 4 and 5), as well as the least disturbed (rank 6) suggesting that even primary forest specialists could recolonise this habitat under the right conditions. I found *Onthophagus haemotopus* Harold, 1875, a small tunnelling species (Horgan 2009) peaked in abundance at intermediate disturbance, and it may be that species such as this need a certain amount of shade and humidity so cannot handle the most exposed habitats, but are otherwise quite tolerant in disturbed areas and may be able to make use of some resources found there, or may take over the niches left by species that had reduced abundances in this habitat type. *Onthophagus rubrescens*, also a tunneller, is thought to be disturbance sensitive and prefer intact forest (Scheffler 2005); I found it in high abundance in mixed history forest, suggesting that small scale disturbances might not severely affect this specialist if the forest is left to regenerate. The small tunneller *Onthophagus*

xanthomerus Bates, 1887 has been described as a habitat generalist but showed a clear decline in abundance from the least to most disturbed habitat.

As well as a shift in dominant species, I identified a loss of rare species with increased disturbance (Figure 3.2). Some of the rare species lost include the large tunnellers *Phanaeus cambeforti* Arnaud, 1982 and *Phaneus chalcomelas* Perty, 1830, the small roller *Scybalocanthon aereus* Schmidt, 1922, the dwellers *Eurysternus wittmerorum* Martinez, 1988 and *Eurysternus foedus* Guérin-méneville 1844 and the small tunneller *Ateuchus connexus* Harold, 1868. A change in community composition can lead to problems of nutrient recycling and other functions if specialist species are lost from an area. This includes the direct effect of dung beetles removing dung and incorporating those nutrients into the soil and removing parasites, reducing soil compaction and improving permeability, which may benefit plant growth, as well as improving soil aeration, resulting in increased plant litter decomposition by other soil fauna (Manning *et al*. 2016).

I found a reduction in the dispersal of small and medium seed mimics as disturbance increased (Figure S3.1). This may be due to a reduction in the diversity of large beetles, as large beetles are likely to carry more beads with the larger quantity of dung they remove. Dispersal of large seed mimics was unaffected by diversity or disturbance, and it is probable that the large beads were dislodged from the dung early in the beetles' digging activity and were too big to be carried with the dung. The loss of secondary seed dispersal is problematic for the successful regeneration of disturbed forests. Primary seed dispersal is often conducted by birds or mammals, who eat the fruit and deposit the seeds in their faeces. This means that the seed deposited are concentrated in a very small area, so have high levels of competition and are exposed to seed predators. This affects seedling survival and leads to reduced seedling recruitment, slowing down the forest recovery process. Dung beetles take the dung and seeds contained within, and they spread these across a wider area and bury them, which improves the chances of seedling survival through reduced competition and predation (Culot *et al*. 2011).

There was no change in dung removal in response to disturbance (Figure S3.1). However, measuring dung removal involved identifying soil and dung particles

and weighing them accurately required prior training and experience, which was not always available. Using dry weights would likely have reduced variation in the data and would be desirable in future studies, but the equipment was unavailable at the time of this study. Dung removal has been found to co-vary closely with seed dispersal (Slade, Mann & Lewis 2011), and it is possible that an effect may have been detected with some improvements to the methodology.

There were no changes in the levels of soil macronutrients in response to disturbance or diversity (Figure S3.2). The high diversity of large dung beetles found in the less disturbed forest was probably important in nutrient sequestration, but this effect was not large enough to detect in the soil analysis. Disentangling the relationship of the ecosystem functions with disturbance rank and diversity is difficult, as the two are strongly correlated. Ecosystem functions likely relate to alpha diversity of dung beetles, but the change in species composition across the gradient also has an important effect (Larsen, Williams & Kremen 2005), and both should be prioritized in conservation efforts to secure optimum ecosystem functioning.

3.6 Conclusion

The effects of human disturbance on biodiversity are complex, and the patterns detected depend on the measures used. In our study of dung beetles, alpha diversity indicated that there was a loss in the number of rare species in the community as disturbance increased. Yet, a loss of species was not the main change taking place across the gradient; most of the change was due to a replacement of species and resulting change in community composition. On inspection of the different functional groups, I discovered that large beetles were more sensitive to forest conversion than smaller species. The effects of disturbance on the seed dispersal functions performed by dung beetles indicate that the impacts on the ecosystem extend beyond a change in the dung beetle community. This study highlights that different diversity measures provide us with specific information and are not interchangeable. To maximise our understanding of the impacts of human disturbance on biodiversity, it is important to consider a holistic approach to biodiversity measurement, including multiple measures of both alpha and beta diversity, and to consider these in the context of the wider ecosystem.

4 Are orchid bees useful indicators of the impacts of human disturbance?

Authors: Laura Allen [a, b], Richard Reeve [a, b], Anna Nousek-McGregor [c], Jaime Villacampa, Ross MacLeod [a].

[a] Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow, UK

[b] Boyd Orr Centre for Population and Ecosystem Health, University of Glasgow, Glasgow, UK

[c] School of Life Sciences, University of Glasgow, Glasgow, UK

Corresponding author: Laura Allen, email: laurajallen@hotmail.com

4.1 Abstract

Biodiversity and ecosystem functions are threatened by human disturbance, and tropical forests are one the most vulnerable habitats. Monitoring the impacts of disturbance and the success of conservation projects is crucial, and to do this effectively it is important to identify suitable measures that are sensitive to ecosystem disturbance. Orchid bees (Euglossini) are a specialist group with mutualistic relationships with many plant species and can fly long distances, making them important pollinators of widely dispersed plant species. A loss of specialist pollinators such as these could have severe consequences for the plants that rely on their services. We therefore aimed to answer the following question: are orchid bees useful indicators of the impacts of human disturbance? If so, what measures of orchid bee diversity are most sensitive? And do orchid bees provide any indication of changes in pollination services along a disturbance gradient? Orchid bees were collected from 18 sites across a gradient of disturbance in a tropical forest region in southeast Peru. Alpha diversity across the gradient was compared using Hills numbers. Beta diversity was assessed using community composition, species contributions to beta diversity, beta diversity partitioning and novel measures of redundancy and representativeness. The potential pollination services available at each site were measured using artificial flowers and counts of pollinator visits. Alpha diversity of orchid bees showed low sensitivity to disturbance. Beta diversity measures were more informative, with disturbed sites found to be highly redundant in the ecosystem compared to the less disturbed sites. However, the most sensitive measure across the gradient was abundance – there was a significant decrease in the number of bees caught as disturbance increased, with likely consequences for pollination services. These results suggest that orchid bees may be useful indicators of the impacts of human disturbance, but alpha diversity is a poor metric for this purpose. In order to understand how human disturbance is affecting biodiversity, multiple diversity indices should be considered, and in the case of orchid bees, redundancy and abundance could be useful for detecting sensitive responses to forest disturbance.

Keywords

Biodiversity indices, indicator, Euglossini, disturbance, agriculture, rainforest.

Introduction

Covering only a small percentage of the world's surface, tropical forest harbours over 50% of terrestrial biodiversity. Yet this cover is decreasing globally, with forest being cut down for timber and conversion to agriculture (FAO, 2015), with severe consequences for biodiversity (Gibson *et al*. 2011; Alroy 2017) and ecosystem functions (DeFries, Foley & Asner 2004). It is therefore of the utmost importance that we have effective tools for detecting changes in biodiversity and ecosystem function in response to anthropogenic disturbance (Pimm & Raven 2000; Kremen 2005; Feest, Aldred & Jedamzik 2010; Hill *et al*. 2016). Indicator groups have been widely used for this purpose (Cleary 2004; Schulze *et al*. 2004; Krug *et al*. 2017), however choosing suitable indicator groups can be challenging (Fleishman & Murphy 2009; Gao, Nielsen & Hedblom 2015; Broszeit *et al*. 2017). Ideally they should be efficient to survey, show a predictable, sensitive response to environmental change, correlate well with overall biodiversity responses and play an important role in the ecosystem (Brown 1997; Hilty & Merenlender 2000).

Bees are the most important group of pollinators (Bawa 1990) but have been declining globally (Allen-Wardell *et al*. 1998; Potts *et al*. 2010), with land conversion and habitat loss the leading causes (Winfree *et al*. 2009). Orchid bees (Hymenoptera: Apidae: Euglossini) are found throughout the Neotropics and are one of the best studied groups of bees in the region. They exhibit many of the recommended features that could make them suitable indicators of disturbance impacts (Brown 1997; Favila & Halffter 1997; Gardner et al. 2008a; Goodsell, Underwood & Chapman 2009), including being widespread, common, cost-effective, easy to sample using standardised methods (Pearson & Dressler 1985) and having well developed taxonomic literature (eg. Dressler 1982a; Roubik 2004; Nemésio & Silveira 2007a). They have close associations with plant species and play important ecological roles as pollinators, able to access flowers that are unavailable to many other insects. They can fly long distances, making them valuable long-distance pollinators (Janzen 1971) for many widely-spaced

plant species and many orchids are entirely dependent on orchid bees for their pollination (Dressler, 1982a). One of the other key features of a good indicator is that they should display a clear, graded response to environmental change. There is some evidence that orchid bees display graded responses to human disturbance, but the results have been mixed and part of our motivation is to study this in greater detail. Orchid bees can persist in heavily degraded ecosystems in some cases, including forest fragments (Storck-Tonon *et al*. 2013) and farmland (Otero & Sandino 2003; Sandino 2004), although this may depend on the proximity to intact forest (Briggs, Perfecto & Brosi 2013). At the same time, there is concern that orchid bees are sensitive to forest loss (Roubik and Hanson, 2004) and some species are thought to be at risk of extinction (Nemesio 2013), which would have major consequences for the pollination services they provide. The importance of resources including orchids and other epiphytes, as well as the sap of specific trees for orchid bees (Dressler, 1982a; Roubik and Hanson, 2004), suggests a mechanism for the loss of orchid bees in disturbed habitats. The loss of old-growth forest and disruption of the canopy is likely to result in a loss of these resources (Hietz, Buchberger & Winkler 2006; Nöske *et al*. 2008), with probable negative consequences for the orchid bee species that depend on them. Together these features suggest that orchid bees could be an excellent candidate for use as an indicator of faunal and floral responses to tropical forest disturbance.

So far, studies on orchid bee responses to forest disturbance have primarily focused on the effects of forest fragmentation, with mixed patterns identified. The abundance and diversity of euglossine bees have been suggested to decline with decreased forest fragment size (Brosi *et al*. 2008; Brosi 2009), however other studies found no effect of fragmentation on abundance or richness (Storck-Tonon *et al*. 2013). A few studies have compared agricultural land to intact forest but these have mostly been focused on less diverse Central American habitats and generally only compared two or three land uses. Briggs *et al*. (2013) found that polyculture could sustain orchid bee communities similar to forest habitats in composition, but abundance was higher in the polyculture than in either forest or monoculture, although abundance did decline with increasing distance from the forest. Abundance and richness of orchid bees have been found to decrease in some agricultural matrix habitats compared to forests

(Aguiar *et al*. 2015), although others have been found to support similar communities to forest (Rosa *et al*. 2015) and some found higher capture rates in agricultural areas than in forest (Otero & Sandino 2003; Sandino 2004). However, studies of forest disturbance gradients are relatively uncommon, and none have covered the response of orchid bees across a continuous, multi-level gradient from monoculture agriculture to intact forest. There are several studies on the mutualistic relationships between orchid bees and orchids (Dressler 1967; Ackerman 1983), but again there is a lack of studies relating orchid bee diversity to overall pollination services available in the ecosystem.

As well as the challenge of selecting suitable indicator groups, another difficulty is deciding how to quantify biodiversity. There are many indices available to measure the alpha, beta and gamma components of diversity. Alpha diversity is usually the main focus of diversity studies, and species richness the most commonly used measure of this because it is intuitive, simple and often sensitive. However, species richness lends a lot of weight to rare species, so other indices such as Shannon and Simpson diversity may be used to shift the weight towards the more dominant species in the community. Recent discussions on diversity partitioning have concluded that diversity profiles (curves simultaneously encompassing many perspectives) based on Hill numbers (Hill 1973) could help avoid a narrow focus on a single result (Jost 2006; Chao, Chiu & Hsieh 2012). Beta diversity is also often of interest in ecological studies but has an even wider array of indices to choose from than alpha diversity (Tuomisto 2010; Anderson *et al*. 2011). Beta diversity measures differ in their approaches to quantifying similarity or dissimilarity between sites, and the importance of species abundance differences, and the relative importance of species turnover or richness differences (Socolar *et al*. 2016). Beta diversity can also be placed into a unified framework for partitioning diversity effectively using diversity profiles (Reeve *et al*. 2016). The large number of diversity measures available have been developed to fit a broad range of questions and few perform consistently well under different conditions, which means that focusing on a single index may risk overlooking important ecological patterns (Santini *et al*. 2017). We are therefore proponents of using multiple measures of alpha and beta diversity to maximise our understanding of biodiversity responses to anthropogenic disturbance.

In this study, we investigated how orchid bee communities respond to habitat conversion across a gradient of human disturbance, from minimally disturbed tropical forest to banana plantations. We aimed to study how alpha and beta diversity changed across this disturbance gradient and aimed to investigate which of the diversity measures used were most sensitive for detecting orchid bee responses to disturbance. By identifying which aspects of the orchid bee community are most sensitive to disturbance, we will be better informed as to which metrics to use when applying orchid bees as indicators of environmental change. Identifying which components of the community respond to disturbance may also help us better understand what they are responding to and pave the way for further investigation into the mechanisms involved. We considered alpha diversity using Hill numbers and used several approaches to quantify beta diversity, including two recently developed measures, redundancy and representativeness (Reeve *et al*. 2016). Finally, we studied the activity of general pollinators across the gradient using artificial flowers. We aimed to identify if there was any change in pollinator activity across the disturbance gradient, and if orchid bee diversity provided any indication of the potential general pollination services available in the ecosystem (Engel & Irwin 2003). We conducted our study in the highly biodiverse Manu Biosphere Reserve, Peru, where there has been limited work on the orchid bee communities, and none to our knowledge on their responses to disturbance.

4.2 Materials and methods

4.2.1 Study area

This study was based around the Manu Learning Centre (-12.789882, -71.391753, 470 m above sea level), a research station run by the Crees Foundation, in the cultural zone of the Manu Biosphere Reserve in southeast Peru, a UNESCO World Heritage Site. This zone contains a mixture of protected areas of lowland tropical forest interspersed with areas of high human impact, including logging and agriculture, and is intended as a buffer for Manu National Park. Eighteen sites were chosen to represent a gradient of human disturbance from banana monoculture to minimally disturbed tropical forest. A stratified site selection approach ensured sampling was not dominated by a single disturbance history, with three sites chosen for each of the six of major land uses in the local area,

covering a gradient of human disturbance (Figure S2.5). These were ranked from highest to lowest disturbance intensity based on land use (Beck *et al*. 2002; Eggleton *et al*. 2002), with 1 being the most disturbed and 6 the least disturbed (as detailed in **Error! Reference source not found.**). For each land use type, o ne of the replicates was named 'A', 'B' or 'C', semi-randomly, taking into consideration suitable site groupings for access and analysis. We sampled all 'A' sites in the first week, then the 'B' and 'C' sites in the following weeks, so that one of each habitat types would be sampled concurrently.

At each site, data were collected on the vegetation structure to assess how this changed across the disturbance gradient. Three vegetation points were randomly selected within each site, and a $25m^2$ plot marked out at each. Within this plot, canopy height was estimated by an individual who had been previously trained using trees of known heights verified with a clinometer, and these estimates were confirmed by a second member of the team. The same person conducted the vegetation measurements at all sites across the gradient to reduce observer bias in the estimates. Canopy cover was quantified using a quadrat held above the sampler's head and the quadrat used to estimate the percentage of canopy cover at five points within the circle. Understorey vegetation density was estimated at the four corners of the sampling plot using the modified Braun-Blanquet scale as described in Hurst and Allen (2007). We counted the number of trees with a diameter >5cm at breast height and measured the diameters of the three largest trees within each vegetation plot, and measured leaf litter depth at 16 random points within the plot. These followed the protocols for vegetation assessment used by Whitworth et al., (2016). Weather data were collected at the research station, with temperature, rainfall and humidity data collected daily at 7am. Elevation data for each site was measured using Garmin GPS devices, and distance to the main river, the Alto Madre de Dios, was measured in QGIS 2.18.7 (QGIS Development Team 2017), measuring the straight line distance from the centre of each site to the nearest edge of the river.

Sites of the different disturbance types were interspersed as much as possible. The potentially confounding effects of large landscape and climatic differences were minimised by selecting sites within a small area (20 km^2), while ensuring sites of the same disturbance type were far enough apart (>500 m) to avoid sampling pseudo-replication (Ramage *et al*. 2013). To minimise spatial effects on

the results we kept groups of sites of different disturbance levels as close together as possible given other constraints and the locations of these habitats. We used linear models to validate the results of our correlation tests and to check for any significant effect of these other environmental variables, including them as explanatory variables along with disturbance if they had any significant effect on the response.

This project was conducted in two parts, the primary study looking at changes in the orchid bee community along the gradient and then a second study exploring potential pollination services across the same sites. We cover the methods and results of the main study first, followed by the pollination study.

4.2.2 Orchid bee diversity

4.2.2.1 Data collection

Orchid bees were sampled in the morning between 09:00-12:00 and in the afternoon between 12:30-15:30 (+/- 15 mins). Each site was sampled for two morning and two afternoon sessions (a total of 12 hours per site) and these four sampling sessions were pooled to form a single sample for each site (a total of 18 samples). To reduce potential biases from weather or other potential temporal sampling biases, two sites were sampled simultaneously - one more disturbed (rank 1-3) and one less (rank 4-6), and on each day different disturbance types were sampled in the mornings and afternoons.

At each site, two sampling stations were set up 50 m apart to reduce any bias from a single within-site location choice. At each of these stations, eight balls of cotton were hung from branches at a height of 1.5 m, with 2 m between cotton balls. Each cotton ball was baited with two drops of one of the following eight attractants: wintergreen oil, methyl salicylate, eucalyptus oil, eucalyptol, vanillin (3 tsp vanillin dissolved in 50 ml 96% ethanol), benzyl acetate, clove oil, eugenol. The bait stations were monitored over the three-hour sampling period, and orchid bees attracted to the baits were caught using hand nets then killed and preserved in 70% ethanol. Orchid bees attracted to the survey area that did not settle at a specific bait but came within 1m of a bait and flitted between baits, were also captured. Multiple researchers conducted the hand netting,

three per site each day. This included trained researchers experienced with capturing insects with nets, and less experienced volunteers. To reduce biases from experience, we ensured that the teams surveying the different sites were as balanced as possible, with less experienced people paired with more experienced people and the teams rotated between the sites.

Preserved orchid bees were identified in Cusco, using a stereo microscope, published keys, checklists and descriptions (Bonilla-Gomez and Nates-Parra, 1992; Dressler, 1978, 1979, 1982b, 1982c, 1982d, 1984; Faria and Melo, 2007; Hinojosa-Díaz and Engel, 2011, 2012, 2014; Kimsey, 1979, 1982; Melo, 2014; Moure, 1965; Nemésio, 2011, 2009; Nemésio and Silveira, 2007b; Niemack et al., 2012; Roubik, 2004; Roubik and Hanson, 2004). For as many species as possible, identification was verified by consulting the collections at the Department of Entomology at the Universidad de San Antonio Abad de Cusco, and at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima. Reference specimens were deposited in both these collections in September 2016.

4.2.2.2 Analysis

A principal component analysis (PCA) of the vegetation structure data across the gradient was performed using the vegan package v.2.4-6 in R (Oksanen *et al.* 2018), and we used a Spearman rank correlation test (Spearman 1904) to check the correlation between disturbance rank and the first principal component of the vegetation PCA.

To test if alpha diversity varied with human disturbance, orchid bee alpha diversity was calculated for each site using Hill numbers, a family of diversity measures parameterised by a viewpoint parameter, q, with increasing emphasis on dominant species as the value of q increases (Hill, 1973; Reeve et al., 2016). We calculated diversity at $q = 0, 1, 2$ and ∞, as these correspond to the following commonly used diversity measures: species richness, Shannon entropy, Simpson diversity and Berger Parker diversity respectively, so our measures can be easily compared to previous studies.

All analyses were conducted using R version 3.3.2 (R Core Team 2017) in RStudio version 1.0.136 (RStudio Team 2016). Observed alpha diversity was calculated

using the package rdiversity v.0.4.3 (Mitchell & Reeve 2016).Estimates of species richness, Shannon entropy and Simpson diversity were calculated using the package iNEXT v.2.0.14 (Hsieh, Ma & Chao 2016) to rarefy or extrapolate estimates to a standard sample size of 50 individuals at each site (Colwell *et al*. 2012; Chao *et al*. 2014). This sample size represented approximately double the smallest sample size, the maximum that can be reliably extrapolated at q = 0 with high confidence (Hsieh, Ma & Chao 2016). This provided approximately 90% sample coverage for all sites (supplementary materials Figure S4.1). The diversity estimates at each value of q were bootstrapped 1000 times using the iNEXT function in R, to calculate a confidence interval around our mean estimates. This allowed us to test for consistency in the direction of change in the diversity estimates while accounting for the uncertainty in the diversity estimates. We did this by extracting the 1000 raw estimates of the diversity of each site, and then calculating the proportion of times a less disturbed site was more diverse than a more disturbed site. All disturbance type pairs were compared, and a Spearman rank correlation test (Spearman 1904) was used to test the correlation between the proportion of times that the less disturbed site was the more diverse of the pair and the difference in disturbance rank between the sites.

To understand how beta diversity was affected by human disturbance, we quantified the change between sites along the gradient using several methods, including community composition, beta diversity partitioning and two recently developed beta diversity measures, redundancy and representativeness (Reeve *et al*. 2016). The total beta diversity of the gradient, measured as the total variance of the community matrix, was calculated using the beta.div.comp function in the R package adespatial v.0.1-1 (Dray *et al*. 2018) along with the partitioning of the total beta diversity into nestedness and turnover. A Hellinger transformation of the species x site abundance matrix was used, as the Hellinger distance provides a good compromise between linearity and resolution and correlates better with ‘true’ distances in simulations than many alternatives (Legendre & Gallagher 2001). Beta diversity decomposition was then calculated for this matrix using the quantitative form of Sorensen’s dissimilarity coefficient, in order to account for differences in relative abundances as well as species identity (Legendre and De Cáceres, 2013). A redundancy analysis (RDA) was used

to examine the change in species composition across the gradient, applied to the Hellinger transformed community matrix and constrained by disturbance rank, elevation and distance to the river, using the vegan package in R (Oksanen *et al.* 2018). The use of this transformation overcomes many of the issues associated with raw Euclidean distances, including many zeros and large differences in abundances, which may lend disproportionate weight to rare species (Legendre & Gallagher 2001; Borcard, Gillet & Legendre 2011). Species contributions to beta diversity (SCBD index), which is the relative degree of variation in the abundance of individual species across the study gradient (Legendre and De Caceres, 2013), were calculated with the beta.div function in the adespatial package, using the Hellinger dissimilarity coefficient (Legendre and De Cáceres, 2013). The abundances of the species with the highest SCBD values were compared across the gradient, with some low SCDB species included for contrast.

The redundancy of the communities at each site was calculated using the redundancy (ρ) measure, available in the package rdiversity (Mitchell & Reeve 2016). This is a measure of beta diversity that represents the extent to which the diversity of the overall metacommunity (the diversity of the whole gradient in this case) would be preserved if a single community or site was lost (Reeve *et al.* 2016). We also calculated the representativeness ($\overline{\rho}$) of the sites, which is a measure of how well a single site represents the overall metacommunity. Representativeness considers how much of the metacommunity diversity a site holds (i.e. the redundancy) relative to the size of the community at that site, providing a correction for the different sample sizes across the gradient. Both redundancy and representativeness were calculated at q = 1, as this provides an intermediate level of conservatism and is a key value of q due to its correspondence to many measures of beta diversity through relative entropy and K-L divergence (Reeve *et al.* 2016).

We used disturbance as a continuous explanatory variable since this allowed us to consider land-use on a continuous spectrum of disturbance intensity, with the possibility of other land-uses falling at intermediate intensities. We could have used an ordered discrete variable, which would have been better able to detect a signal in the presence of unevenness in disturbance differences, but this would

have required more data to fit. Our simpler approach is supported by the strong correlation of our continuous disturbance rank with vegetation structure data. Nonetheless, because we could not be sure of the exact difference in disturbance between each level, where possible we used a Spearman rank correlation test to assess the patterns of diversity along this gradient. This approach makes no assumptions regarding the shape of the relationship between the variables, only that the pattern is monotonic along the gradient, and is a therefore a conservative approach for these analyses. Spearman rank correlation tests were used to test for correlations of disturbance rank with abundance, observed alpha diversity at $q = 0$, 1, 2 and ∞, estimated alpha diversity at $q = 0$, 1 and 2, and representativeness and redundancy at $q = 1$. In addition to checking each value of q independently, we tested if the overall pattern of alpha diversity change across the disturbance gradient was significant at $\alpha = 0.05$. To overcome the non-independence of the q values from one another, we used a permutation test to calculate the combined p value for the correlation between disturbance rank and observed alpha diversity at $q = 0$, 0.5, 1, 2 and ∞ and estimated alpha diversity at $q = 0$, 0.5, 1 and 2 ($q = \infty$ could not be included because the estimates all converged at 1, so there was no variation; we included $q = 0.5$ because q is on a logarithmic scale, so this prevents biased weighting of rare species when calculating the overall pattern of alpha diversity across multiple values of q). The permutation test involved randomly re-labelling the study sites, and then re-calculating the significance of the correlation between disturbance rank (now randomly re-assigned) and alpha diversity at each value of q (Good 2000). These permuted p-values for each value of q were combined to determine the significance of the overall alpha diversity change across the gradient (Fisher 1925). This was repeated for 10000 permutations, and the permuted p-values compared to those obtained with the original data, to determine the probability that the observed correlation of diversity could have occurred by chance. To check that the patterns of change in redundancy and representativeness across the gradient were not specific to our chosen value of $q = 1$, we also used a permutation test to obtain the combined p value for the correlation of disturbance rank with redundancy and representativeness calculated at $q = 0$, 0.5, 1, 2 and ∞.

As well as testing for the effect of disturbance on diversity and abundance, the potential effects of altitude, rainfall and distance to river were investigated using linear models, to confirm whether the effects of disturbance identified with the correlation tests remained significant when accounting for these variables. The diversity and abundance response variables were log-transformed and modelled with a gaussian distribution. The model summaries and residuals were inspected to evaluate model fit. None of the additional environmental variables resulted in a significant improvement compared the model that included only disturbance rank. Full details of the models tested can be found in Table S4.2 of the supplementary materials. In the case of the relationship between abundance and disturbance rank, visual inspection of the data prompted us to also test a quadratic polynomial, but the AIC values indicated that a linear relationship was a better fit (ΔAIC = 1.42). Throughout the results section, the statistics reported are the results of the Spearman rank correlation test unless stated otherwise.

4.2.3 Pollination services

4.2.3.1 Data collection

The potential for the provision of pollination services (from any pollinators) across the gradient was tested using artificial flowers filled with sugar solution (Internicola *et al.*, 2007; Real, 1981). The flowers were 5 cm in diameter and constructed from thin craft foam with a central well containing 1.5 ml of the sugar solution (1:1 sugar and water). Red, blue and yellow flowers were used, with five of each colour on an array that was suspended at a height of 1.3 m at the survey site. Two flower arrays (30 flowers in total) were used at each site, separated by approximately 30 m, and each monitored by a member of the research team. All insects (of any Order) that arrived at the flower array were counted as potential pollination events, apart from individuals that simply moved from one location on the array to another. The flowers were monitored for three periods of 45 minutes separated by 15-minute intervals during which the flowers were covered. This was repeated for four mornings, between 08:45 and 13:00, at each of the 18 sites.

4.2.3.2 Analysis

Spearman rank correlation tests were used to test the correlation between the number of potential pollination events (flower visits) with disturbance rank and with observed orchid bee species richness.

4.3 Results

4.3.1 Orchid bee diversity

4.3.1.1 Vegetation structure

The first component of the vegetation structure PCA (PC1) explained 37% of the variation in vegetation structure, with higher rankings (lower disturbance) correlated positively with canopy height and canopy cover, tree count and diameter, and negatively with leaf litter depth and understorey herb abundance (Figure 2.3). There was a strong correlation between vegetation structure (PC1) and disturbance rank, supporting the disturbance ranking used to represent human disturbance intensity along the gradient ($p < 0.00001$, $rho = 0.92$; Figure 4.1). The results of all correlation tests are provided in Table S4.1 in the supplementary materials.

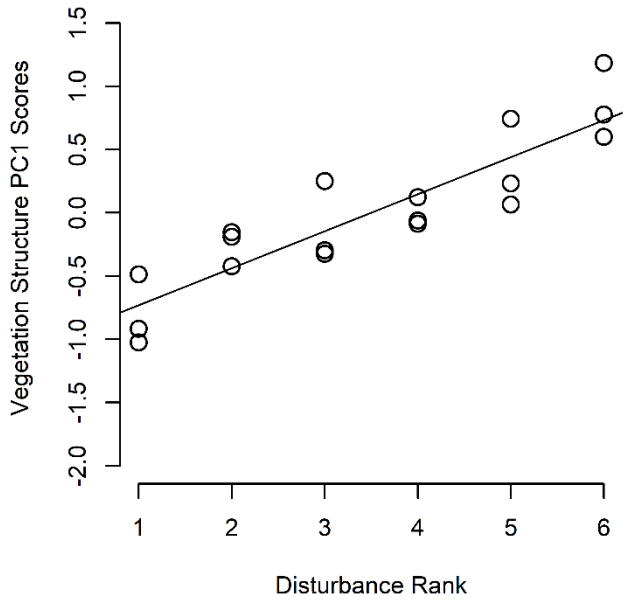

Figure 4.1 Correlation between vegetation structure and disturbance rank. Disturbance rank runs from the most disturbed (rank 1) to the least disturbed habitat (rank 6). Line indicates best fit of the correlation between disturbance rank and vegetation structure (PC1). The first axis of the principal component analysis of vegetation structure was positively correlated with canopy height, canopy cover, tree count and diameter, and negatively with leaf litter depth and understorey herb abundance.

4.3.1.2 Alpha diversity

We collected 1783 individuals of 31 species of orchid bee. Overall observed alpha diversity decreased across the disturbance gradient (permuted combined p value for q = 0, 0.5, 1, 2 and ∞: p = 0.025; Figure 4.2). This was mostly driven by the patterns of alpha diversity at low values of q, with observed species richness (q = 0) and observed Shannon diversity (q = 1) both decreasing with increased disturbance across the gradient (rho = 0.57, p = 0.01; rho = 0.51, p = 0.03). There was no significant change in alpha diversity across the gradient at higher values of q. However, when estimated diversity was examined, correcting for sample size (n = 50), there were no significant differences in estimated diversity across the disturbance gradient, either overall (permuted combined p value for q = 0, 0.5, 1 and 2: p = 0.330) or for any individual value of q, due to the wide confidence intervals around the mean estimates (Figure 4.3 and Figure S4.2).

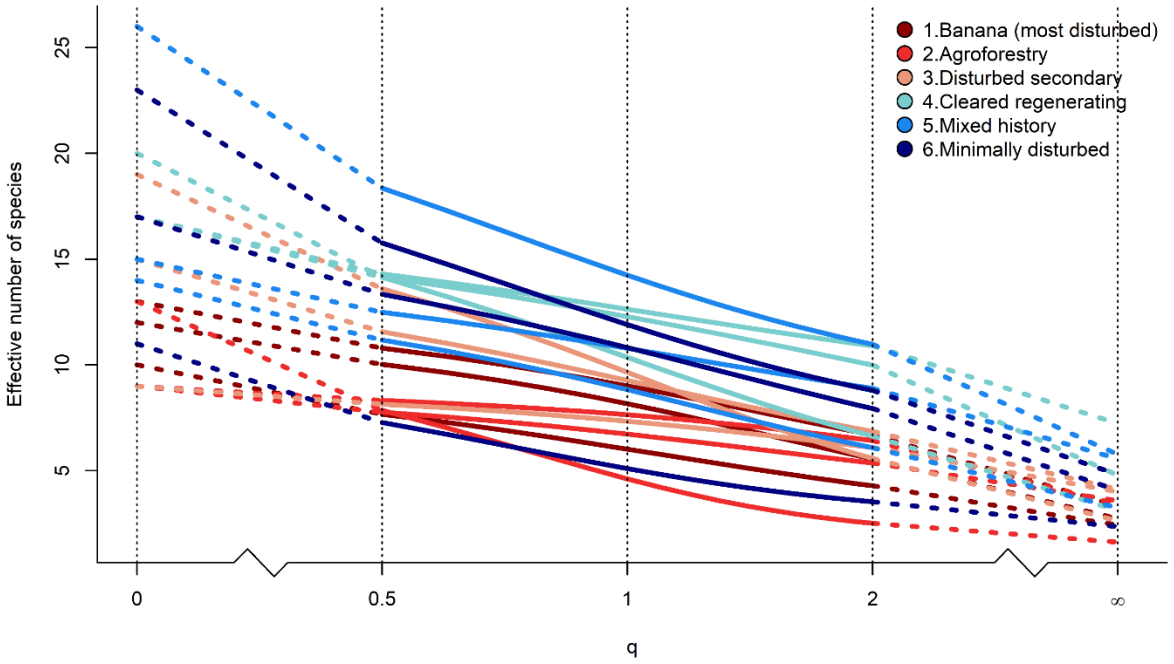

Figure 4.2 Orchid bee observed alpha diversity across the disturbance gradient. Increasing values of q indicate increased emphasis on dominant species (q = 0 = species richness, 1 = Shannon diversity, 2 = Simpson diversity, ∞ = Berger Parker diversity). Disturbance rank is shown by a colour gradient, dark red for the most disturbed sites, dark blue for the least disturbed. Overall diversity was significantly higher in less disturbed sites (permuted combined p value = 0.025), and at q = 0 (rho = 0.57, p = 0.01) and q = 1 (rho = 0.51, p = 0.03), but not significantly different at or above q = 2 (rho = 0.45, p = 0.06) Because q is on a log scale, the broken axis and dashed lines indicate inferred values as diversity was calculated only for the values at either side of the break (0 and ∞); along the solid line, q was calculated at intervals of 0.1.

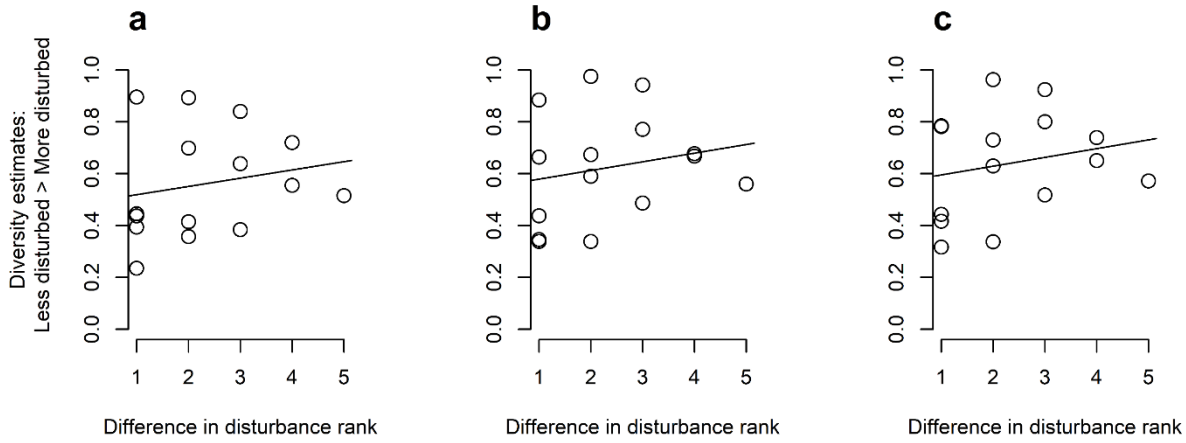

Figure 4.3 Correlation between diversity estimates and disturbance ranking. The proportion of times that the less disturbed habitat was estimated to have a higher diversity than the more disturbed habitat, based on 1000 estimates calculated using the iNEXT package in R, and comparing between all possible habitat pairs. High values along the x-axis mean the sites are further apart along the disturbance gradient (with added jitter). Panel a shows the relationship for q = 0, b for q = 1, and c for q = 2; n = 50. A best fit line is shown for the correlation between the proportion of times the less disturbed sites is more diverse with the difference in disturbance ranking between sites.

4.3.1.3 Abundance

Abundance of orchid bees declined across the disturbance gradient (rho = 0.63, p = 0.005), with less than a quarter of the number of bees found in the most disturbed habitat compared to the best of the less disturbed forest sites (Figure 4.4).

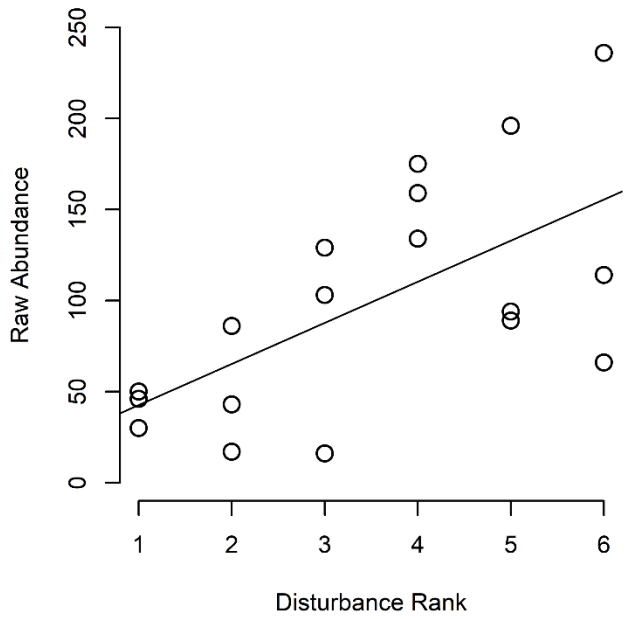

Figure 4.4 Change in orchid bee abundance across the disturbance gradient. Abundance is the number of orchid bees captured at each site, plotted against the disturbance rank of the site. Disturbance rank runs from 1 (most disturbed) to 6 (least disturbed). A best fit line shows the correlation between abundance and disturbance rank.

4.3.1.4 Beta diversity

Although there was some change in the number of orchid bees species found across the disturbance gradient, beta diversity was driven primarily by a turnover of species, rather than a change in richness. The results of the beta diversity partitioning were a total beta diversity of 0.18 across the gradient (a total beta diversity of 1 would indicate that the sites had completely distinct communities; Legendre & De Cáceres 2013), with 77% of this due to species turnover and 22% due to differences in richness (nestedness).

The composition of the orchid bee community changed across the gradient, with different communities found in the more and less disturbed sites, as demonstrated by a separation along the RDA1 axis (Figure 4.5), which captured

37% of the variation in community composition. The Species Contributions to Beta Diversity (SCBD) index identified the species that changed most in abundance along the gradient (Figure 4.6). *Euglossa chalybeata* and *Euglossa orellana* appear to be forest specialists that are lost as forest disturbance increases, whereas *Euglossa despecta* appears to favour intermediate levels of disturbance.

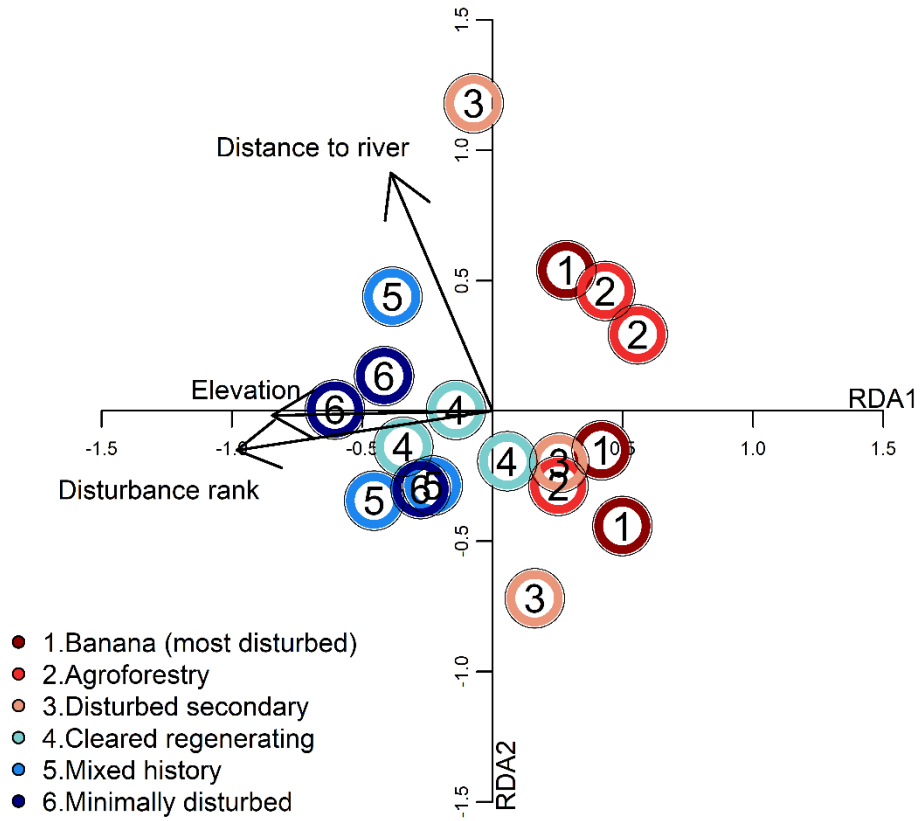

Figure 4.5 RDA of orchid bee community composition across the disturbance gradient, constrained by disturbance rank, elevation and distance to the river. Disturbance rank is represented by a colour gradient from dark red (most disturbed) to dark blue (least disturbed), with the rank of each site also shown numerically.

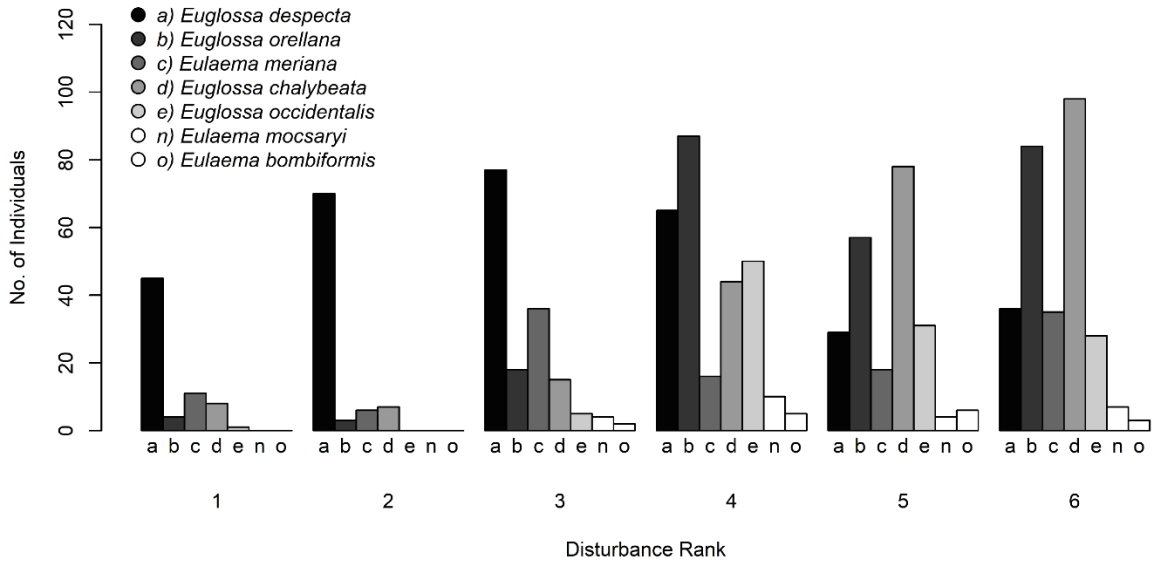

Figure 4.6 – Differences in abundance across the gradient of the species that contribute most to beta diversity. A total of 31 species were found. The grey bars (a-e) show the top five contributors to beta diversity, in order of contribution. Two examples of low contributors to beta diversity are shown in white (n and o) for comparison. Disturbance rank runs from 1-6, with 1 representing the most disturbed sites.

The less disturbed sites hold communities that are less redundant (Figure 4.7a; at q = 1: p = 0.02, rho = -0.55; permuted combined p value for q = 0, 0.5, 1, 2 and ∞: p = 0.016) and more representative of the overall metacommunity (Figure 4.7b; at q = 1: p = 0.04, rho = 0.4922; permuted combined p value for q = 0, 0.5, 1, 2 and ∞: p = 0.024) than the more disturbed sites. This suggests that the overall diversity of the region (all sites across the gradient) would suffer a greater loss should the community of one of the less disturbed sites be lost, than if the community of a highly disturbed site was lost.

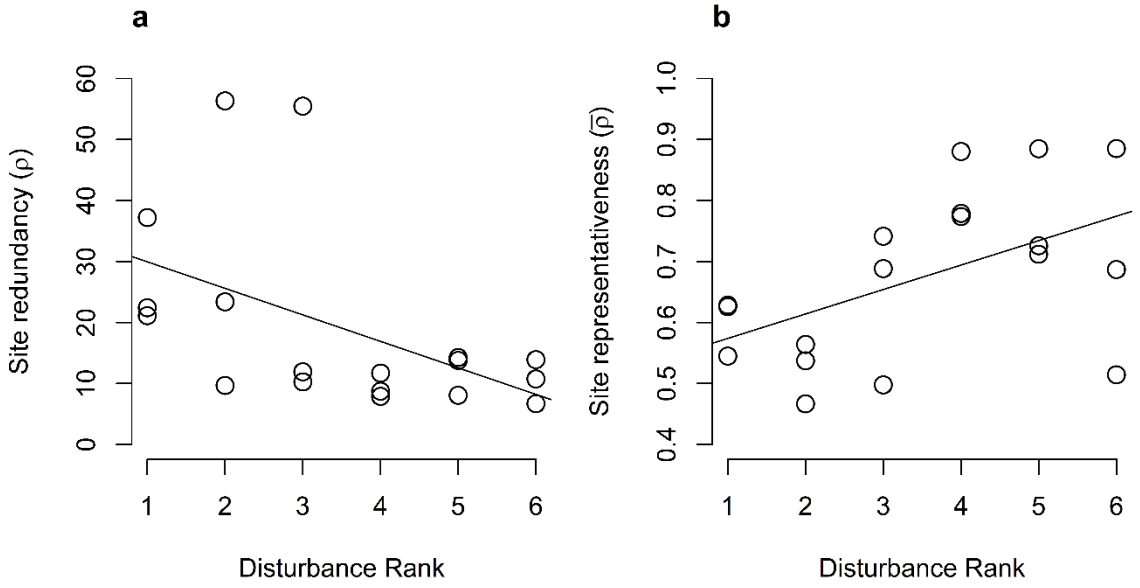

Figure 4.7 Change in the a) redundancy (ρ) and b) representativeness ($\bar{\rho}$) of sites (at q = 1) across the disturbance gradient. The disturbance rank runs from 1 (most disturbed) to 6 (least disturbed) and lines of best fit indicate the correlations

4.3.2 Pollination services

There was no relationship between the number of visits from potential pollinator insects and disturbance rank (Figure 4.8a; rho = 0.1160, p = 0.6467) or orchid bee diversity (Figure 4.8b; rho = -0.19, p > 0.4 at q = 0, 1 and 2). The artificial flowers received similar numbers of visits across the disturbance gradient, with slightly more visits occurring in lower disturbance sites but with a large amount of variance within each disturbance level. We found no evidence that orchid bee diversity (specialised pollinators) indicated any trend in the activity of pollinators in general.

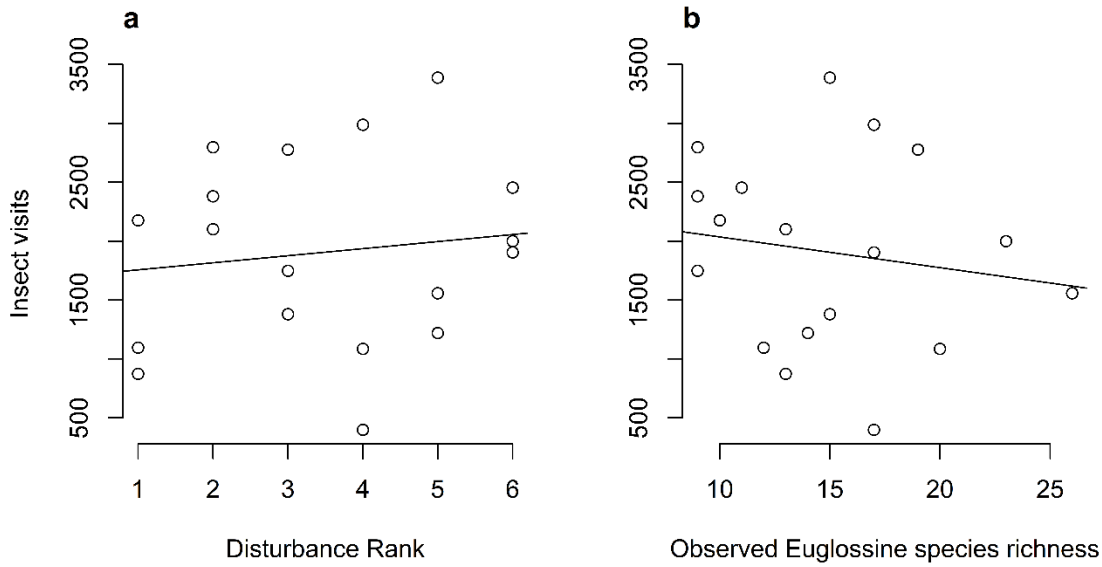

Figure 4.8 Potential pollination events. Number of insect visits to artificial flower arrays correlated **with** (a) disturbance rank and (b) observed orchid bee species richness (q = 0). Disturbance ranking runs from 1 (most disturbed) to 6 (least disturbed). Correlations between insect visits and disturbance or richness are each indicated by a line of best fit.

4.4 Discussion

Orchid bees declined in abundance as disturbance increased, and community composition changed across the gradient, suggesting that orchid bees can be useful as indicators of the impacts of human disturbance. Redundancy of the orchid bee community at a site increased with increased disturbance and representativeness of the sites decreased. No changes in species richness and higher order alpha diversity could be detected after controlling for sample sizes suggesting that, unlike many other groups, alpha diversity of orchid bees is unlikely to be a strong indicator of human disturbance impacts. We found no change in pollinator visits in response to disturbance nor any correlation between pollinator visits and orchid bee species richness.

Previous studies that suggested orchid bees show little response to human disturbance focused on different disturbance types and fewer sites with less replication than covered in our study (Nemésio & Silveira 2006; Rasmussen 2009). The first of these studies sampled a similar number of bees as in our study over a longer period in only six sites, focusing on the effect of distance to the forest edge. They found no change in observed species richness, and erratic differences in abundance, uncorrelated with distance to edge, but they did find some change in community composition, though many species were shared across sites (Nemésio & Silveira 2006). The second study considered alpha

diversity at q = 0, 1 and 2 as well as abundance and community similarity between sites and found no significant relationship between any of these with disturbance level (Rasmussen 2009). However, only three sites were compared, one of each disturbance type: primary forest, a reforested site and one heavily disturbed forest. Like these studies, we also found no significant change in alpha diversity after controlling for sample size. However, it should be noted that this lack of a significant response appeared to be because there were many more bees caught in the less disturbed sites, consistent with the marked decrease in orchid bee abundance with increased disturbance we detected. When comparing observed alpha diversity, without controlling for the number of bees caught, there was a decrease in species richness and Shannon diversity as disturbance increased. Since standardised sampling effort was used there is no reason to suspect the observed differences were caused by any bias in the sampling design, and so this difference should not be dismissed. That there are fewer bees in the disturbed sites means that the confidence interval around the estimated true number of species present is large, however if sampling time was extended to catch the same number of bees as found in the least disturbed sites, it would be unsurprising if there were still fewer species (Figure S4.2). In any case, the fact that during a set time period, fewer individuals of fewer species are likely to visit plants in disturbed habitats is an ecologically meaningful result, as it is likely to impact plant pollination, even if similar total numbers of species could eventually be detected over a longer time.

This kind of study is prone to problems with biases arising from study design and the assistance of volunteers. As well as training, and pairing experienced staff with inexperienced samplers, we randomised the location of the teams to avoid systematic biases. The high turnover of volunteers allowed us to keep this strategy constant over the sampling period. Capture success was high, and although there were some escapes, many of these individuals could be seen leaving and returning to the bait, allowing a second capture attempt. We did not record miss rates but there was no noticeable difference observed between genera or species identifiable in flight, although this would be valuable to investigate in future studies. Another known issue in studies like this is the potential for differences in the attractive radius of the baits between sites to affect capture rates, because differences in vegetation structure and shade

between the sites could affect the evaporation rates and how much the baits might be carried on the wind. Further research is needed to fully address this (Nemésio 2012), but we followed standard practice from previous studies in using standardised bait protocols across all sites, which included regularly refreshing the bait to avoid evaporation rate issues. Since there was a higher capture rate overall in the less open forest, there was also no evidence for sampling issues related to scent dispersal being inhibited by vegetation. Due to this study region consisting of a matrix of different habitat types, including small-scale agriculture, it was unavoidable that some sampling sites would not be far from other disturbance types. We set up the bait stations near the middle of a habitat type to ensure that the majority of bees were likely to be attracted from within that site and ensured a minimum of 100m to the neighbouring habitat. However, it is plausible that some bees may have been attracted from neighbouring habitats, yet this should theoretically weaken our power to detect a correlation between the orchid bee community and habitat type, lending confidence to the patterns that we have detected, as discussed in Brosi (2009). Furthermore, for ecological purposes we care about the bees that visit a site to provide ecosystem services (pollination), so if some of these visit from neighbouring habitats that is still of relevance, as we are interested in the impacts on the orchid bee community in the context of this matrix landscape.

Regarding the value of orchid bees as indicators, in this study we have shown that changes in the orchid bee population are strongly correlated with intensity of forest disturbance, and identified which measures are most useful for detecting these responses. The results of the vegetation surveys showed a loss of canopy cover and reduction in canopy height and number of trees as disturbance increased (Figure 2.3). This may also result in a change in microclimate and a loss of epiphytes. A loss of resources such as nectar and nesting habitats may have contributed to the decline in orchid bee abundance, whereas a change in the species of epiphytes and other plants present could have influenced the change in orchid bee species composition along the gradient. A more detailed exploration of the mechanisms behind the orchid bee responses are important in order to understand what exactly they are indicative of: is it a change in vegetation structure (shown to be closely correlated with disturbance in our study), a decline in overall biodiversity, a loss of important nesting habitats, a

loss of epiphytes or particular flower species? These are important points for further investigation, as there is a general lack of information about the relationship between ecological indicators and indicandum (Gao, Nielsen & Hedblom 2015).

Species richness has been recognised as a poor index for detecting the effect of disturbance on some other taxonomic groups, and it has been suggested that in many cases community composition may be more sensitive (Stork *et al*. 2017a). For example, Samejima *et al*. (2004) found that stingless bees (Meliponini) showed a change in community composition in response to human disturbance. We also found that community composition changed across the disturbance gradient, however, community composition can be expected to change for many reasons, including non-disturbance related changes in vegetation and other habitat features. Due to the small spatial scale of this study and the history of the area, we expect that the habitats of the study sites would have been very similar prior to the anthropogenic disturbance; this assumption is less likely to hold true across larger spatial scales, making it harder to link changes in species composition to habitat disturbance across space. However, as a potential indicator, identifying the key shifts in the orchid bee community composition in response to disturbance could be useful for monitoring a site over time, to provide an indication of whether the site is being disturbed to a degree that is negatively impacting the ecosystem (Santini *et al*. 2017).

In ecological terms, reduced orchid bee abundance in highly disturbed habitats is of concern, as it is indicative of a potential cascade effect resulting from the loss of forest canopy, along with habitat complexity and epiphytic diversity (Barthlott *et al*. 2001). This could result in a loss of specialist pollinators that are crucial for the persistence of many plant species, which may reduce the resilience of the remaining degraded forest, as the ecological networks have been weakened. However, the services provided by orchid bees may be partially maintained by a well-connected patchwork of habitats including high quality forest, as the dispersal distances of this group (Janzen 1971) enables them to make opportunistic visits to degraded habitats when resources are available. This way, they may be able to provide pollination services to habitats that possibly lack the resources to support viable orchid bee populations

independently, but this will require a substantial area of intact forest to be maintained nearby.

We found that the redundancy (ρ) of the sites increased with increased disturbance. Redundancy is therefore likely to be a useful measure of disturbance impacts, because it considers both the species present and their abundance, so gives a more complete picture of how the sites differ. From these results, we can see that the impact of losing a minimally disturbed site would more severely impact the overall diversity of the region than the loss of a highly disturbed site. Similarly, when we considered the representativeness ($\overline{\rho}$) of the sites at q = 1, we found that in each of the less disturbed sites (ranks 4-6) about 80% of the overall biodiversity of the study area could be found, on average, whereas the more disturbed sites (ranks 1-3) only held an average of about 60%.

Pollination potential showed no correlation with orchid bee abundance or alpha diversity (Figure 4.8; supplementary materials Table S4.1). This is probably because visitors to the flower arrays were mostly sweat bees (family Halictidae) and these visited the flowers in high abundance. Other visitors included flies, wasps, butterflies, a few orchid bees, and even a hummingbird on one occasion. An important caveat in interpreting this experiment was that we were only able to measure the potential opportunities for pollination (the number of visits the flower received), and were not able to account for the fact that insects differ widely in their effectiveness as pollinators (Primack & Silander 1975; Schemske & Horvitz 1984; Ramsey 1988; Ivey, Martinez & Wyatt 2003; King, Ballantyne & Willmer 2013). Turnover of species between sites also means that higher bee diversity than expected is likely to be required to deliver pollination services over large spatial scales (Winfree *et al.* 2018). Halictid bees are considered valuable pollinators and visit many different plant species (Lindsey 1984), although they do not show such distinctive host adaptations as the orchid bees. Orchid bees do pollinate a wide range of plants; however, they are particularly important due to their many species-specific relationships and cannot be easily substituted by more generalist pollinators.

4.5 Conclusion

Orchid bees show a clear negative response to human disturbance across a tropical forest-agricultural gradient. They are also efficient to sample and play a key role in pollination services. We therefore suggest they can be a useful addition to the indicator groups available for studying the impacts of forest loss on biodiversity and ecosystem functioning. In choosing whether to use orchid bees in future biodiversity studies it should be born in mind that it is often important that more than one indicator group be considered in any assessment (Lawton *et al*. 1998; Hilty & Merenlender 2000). When orchid bees are selected as a suitable indicator group, our results show that abundance, redundancy (ρ) and representativeness ($\overline{\rho}$) provide the most sensitive measures for detecting the response of orchid bees to human disturbance. In order to understand the response of biodiversity to human disturbance, it is essential to consider the response measures carefully, as a measure that works well for one group may not always be the best for another, and often multiple indices are necessary.

4.6 Data Access

The data have been made publicly available and can be accessed from the University of Glasgow Enlighten repository:
http://dx.doi.org/10.5525/gla.researchdata.589

5 Exploring the use of similarity-sensitive diversity measures for detecting the impacts of human disturbance: a case study on neotropical butterflies.

5.1 Abstract

Tropical forests are globally threatened by human disturbance, including logging and conversion to agriculture. In order to assess the impact of such disturbances, to quantify the effectiveness of conservation measures and to evaluate the success of restoration projects, it is necessary to have reliable tools for quantifying biodiversity change. Indicator taxa such as butterflies are often used for such purposes, but there is no consensus on the most suitable diversity indices to apply, which can lead to conflicting response patterns being detected. Here I explore a new family of diversity measures, which extensively cover the alpha, beta and gamma diversity components in a single coherent framework. These measures also allow the similarity between species to be considered in the analysis (an aspect of diversity that has often been neglected in conservation assessments before now). I collected and analysed data on butterfly diversity across a gradient of human disturbance in the Peruvian Amazon, from near-pristine forest to monoculture plantations. Butterflies were found to show negative responses to human disturbance in both alpha and beta components of diversity. Redundancy of the sites was lowest in the less disturbed forest, highlighting the importance of these areas for conservation. Incorporating species similarity resulted in different diversity patterns being detected and allowed us to unpick some of the drivers of the observed biodiversity changes. Our results demonstrate the need to use multiple diversity measures and to identify clear assessment goals to avoid overlooking important patterns of biodiversity change.

5.2 Introduction

Monitoring biodiversity is essential for understanding the impact that human disturbance is having on global ecosystems (Pimm & Raven 2000), including their structure, function and resilience (Hooper *et al*. 2005). Tropical forests are one of the most threatened ecosystems in the world, and home to the majority of

the world's terrestrial biodiversity (Bradshaw, Sodhi & Brook 2009; Gibson *et al.* 2011). One of the major forms of disturbance of tropical forest is clearance for agriculture, with negative consequences for both global and local biodiversity (Newbold *et al.* 2015; Gonzalez *et al.* 2016). However, there is hope that, if allowed to regenerate under suitable conditions (Whitworth *et al.* 2016b), forests may be able recover their pre-disturbance levels of biodiversity and ecosystem functioning (Newbold *et al.* 2015). There are also moves to develop less damaging forms of agriculture, such as agroforestry systems that include a mix of native tree species in between the crop plants, providing shelter for wildlife as well as a sustainable source of timber (Montagnini *et al.* 2005). To identify whether or not these forests can indeed recover successfully, it is necessary to monitor them either through time (pre and post disturbance, and during the recovery period) or across space (comparing disturbed, regenerating and pristine habitats). The most common approaches for such biological monitoring are collecting measurements on vegetation structure (Wikum & Shanholtzer 1978; DeWalt, Maliakal & Denslow 2003) and the biodiversity of indicator taxa that are thought to be representative of overall biodiversity patterns (Kati *et al.* 2004; Thomas 2005; Pinto *et al.* 2008; Lewandowski, Noss & Parsons 2010) or specific ecosystem functions (Braga *et al.* 2013; Gagic *et al.* 2015).

As there are so many ways to measure biodiversity, it can be challenging for a researcher to choose an appropriate one. The most suitable metrics may depend on both the taxonomic group studied and the aim of a project. There is no consensus on the best diversity measures to use when assessing the responses of butterflies or other indicator groups to environmental change (Hill *et al.* 2016), and in some cases contrasting results may be uncovered depending on the metric used (Hamer *et al.* 2017). Species richness is one of the most commonly used biodiversity measures (e.g. Alroy 2017; Barlow *et al.* 2007; Newbold *et al.* 2015), as it is easily understood and comparable and it places equal weight on rare species, which are often of importance for conservation (Villalobos *et al.* 2013; Hubbell 2013). However, in some cases it may be beneficial to place less emphasis on rare species, such as in the context of biodiversity effects on ecosystem functioning (Walker, Kinzig & Langridge 1999) or when communities can be distinguished by identifying only the most common species, thereby

making efficient use of resources (Caruso *et al*. 2007), so it is important to consider other measures. Species richness and abundance have been found to be the most sensitive measures for detecting responses to environmental change, but these are associated with decreases in evenness, which results in compound measures, such as Shannon diversity, being less sensitive for detecting responses to changing environmental conditions (MacDonald, Nielsen & Acorn 2017). However, it is important to note that richness, abundance and evenness convey distinct, valuable information on the community assemblage, and a single measure will often not be sufficient to assess all the properties of the species diversity of a community. Hill numbers provide a valuable tool for this assessment, presenting multiple perspectives for biodiversity analysis within a consistent framework (Hill 1973).

Most field-based biodiversity studies focus on alpha diversity, but this overlooks any change in community composition between samples, which in many cases is essential to consider (Hillebrand *et al*. 2017; Stork *et al*. 2017). Community composition, similarity and other beta diversity measures can provide valuable insights into the responses of habitat specialists and some of the mechanisms behind the biodiversity patterns observed (Legendre, Borcard & Peres-Neto 2005; Novotny *et al*. 2007; Ribeiro *et al*. 2008; Dahl *et al*. 2009; Socolar *et al*. 2016). Another important point to consider in biodiversity measurement is that not all species are equally distinct (Burghardt & Tallamy 2015). Some are closely related, share very similar functional niches (Luck & Smallbone 2011), or exhibit very similar morphology (de la Maza & Soberón 1998) and this is generally overlooked. Recent developments in biodiversity measurement allow the similarity of species to be incorporated into the diversity indices (Leinster & Cobbold 2012). This advance may be important for distinguishing and understanding communities that have been affected by different types or intensities of disturbance.

The diversity measures used in this study are primarily those developed and described by Reeve *et al*. (2016). These measures are based on Hills effective numbers (Hill 1973) and Leinster and Cobbold's similarity-sensitive diversity (Leinster & Cobbold 2012), both originating from Rényi's generalised entropies (Rényi 1961). These measures incorporate a viewpoint parameter, q, which reflects the importance of the relative abundance of species in the community.

Larger values of q tend to provide more conservative diversity measures. For example, in the case of alpha diversity, q = 0 is the equivalent of species richness, where all species contribute equally to the diversity index no matter how rare or common they are in the community. At the other end of the spectrum at q = ∞, equivalent to Berger-Parker diversity (Berger & Parker 1970), only the most dominant species contribute to the diversity index and rare species are excluded. Alpha, beta and gamma diversity can all be calculated within this new framework, and it is possible to calculate the diversity of both the metacommunity and its constituent subcommunities. This suite of measures has the flexibility to be used both in its naïve form, where all species are considered equally distinct, or can account for species similarity. Species similarity is defined by a user-specified similarity matrix, which can be tailored to the type of similarity of most interest (e.g. taxonomic or functional). If phylogenetic similarity is used, Reeve *et al*.'s 2016 measures are closely related to other phylogenetic diversity indices such as those developed by Chao, Chiu & Jost (2010), or Faith's phylogenetic diversity (Faith 1992) at q = 0 (Leinster & Cobbold 2012). If functional similarity is used, they can provide a measure of functional diversity, as used by Sarker *et al*. (2016). One of the main advantages of this new set of diversity measures is that it provides a flexible approach to incorporate almost any type of similarity into a mathematically consistent system covering alpha, beta and gamma diversity from multiple perspectives using effective numbers. Other types of functional and phylogenetic diversity are calculated in a range of ways not directly related to one another, often fail to incorporate information on species abundances, and the numbers produced may be difficult to interpret (Leinster & Cobbold 2012). The use of diversity profiles and species similarity as advocated by Leinster and Cobbold (2012) have so far been applied to a wide range of problems (Saunders, Luck & Mayfield 2013; Veresoglou *et al*. 2014; Vuono *et al*. 2015; Tucker *et al*. 2016; Zhang, Rousseau & Glanzel 2016), but this study is the first time they have been used to assess the response of biodiversity across a human disturbance gradient in neotropical rainforest.

In this study, I use the recently developed diversity measures described above to explore the responses of neotropical butterflies across a human disturbance gradient. Butterflies are one of the best studied groups of invertebrates in the

tropics. They play important roles in herbivory *(*Muto-Fujita *et al*. 2017; Tiple *et al*. 2011), pollination (Cruden & Hermann-Parker 1979; Courtney, Hill & Westerman 1982) and nectar theft (Bauder, Warren & Krenn 2015). Their close relationships with their host plants and changing resource requirements at different life stages mean that changes in butterfly communities could indicate an underlying change in available resources (Brown & Hutchings 1997; Brown & Freitas 2000). Butterflies also hold appeal as indicators due to ease of sampling and identification, their rapid generation time and global distribution and sensitivity to environmental change (Brown 1997), as well as their charismatic nature (Fleishman & Murphy 2009). Butterflies have been widely used as indicators of the impacts of changing environments, including climate change (Hill *et al*. 2002), logging (Cleary 2004) and forest fragmentation (Shahabuddin & Ponte 2005), and are frequently used as a model taxon to represent insect faunal responses to environmental change (Brown 1997).

Butterflies are sensitive to changes in vegetation structure and microclimate (Kremen 1992), and they rely on a broad range of food plants suggesting that they are likely to respond to changes in the availability of these resources (DeVries, Murray & Lande 1997). However, they have also been found to show limited correlation with anthropogenic disturbance and plant diversity (Kremen 1992; Hawkins & Porter 2003), and poor correlation with other taxonomic groups (Lawton *et al*. 1998; Ricketts, Daily & Ehrlich 2002; Hayes *et al*. 2009), although they may correlate better than other potential indicators (Syaripuddin, Sing & Wilson 2015). In some cases, fruit feeding butterflies have been used as surrogates of all butterflies, and in turn of all insects (Daily & Ehrlich 1995), yet the validity of these relationships has not been fully tested. Being phytophagous, butterfly populations are closely tied to changes in light, humidity, nutrient availability and plant growth cycles, and therefore any fluctuations in butterfly abundances may indicate changes in the plant communities and related elements of the ecosystem that may be more time-consuming or difficult to detect directly (Brown 1997). However, the value of butterflies as indicators is debatable, since despite many studies discussing butterflies in the context of their role as indicators, many of the environmental characteristics with which butterfly species are associated can be measured directly and there is a lack of evidence as to how well butterflies indicate changes in biodiversity or any aspect

of biological functioning (Fleishman & Murphy, 2009). Yet butterflies continue to be one of the best studied invertebrate groups, and while further work is needed to verify their role as indicators, a loss of butterflies in response to human disturbance remains of both conservation concern and ecological interest.

In response to anthropogenic disturbance, including logging and conversion to agriculture, butterfly communities have been found to show a decrease in species richness (Schulze *et al*. 2004; Barlow *et al*. 2007b) and a shift in community composition, with a loss of forest specialists and an increase in generalist species (Molina-Martínez *et al*. 2016; Hamer *et al*. 2003). However, other studies have also uncovered an increase in species richness with increasing disturbance (Kudavidanage *et al*. 2012), so while this group appears to be sensitive to disturbance, their responses are not always consistent.

In this study, I therefore aimed to identify how butterfly diversity changed across a human land use gradient in the Peruvian Amazon. I also aimed to test if recent advances in biodiversity measurement can add valuable insights into patterns of biodiversity change in response to human disturbance and consider the implications of this for conservation. Specifically, I aimed to examine the patterns of diversity observed using four different measures based on Hill numbers: alpha diversity, redundancy and representativeness (measures of beta diversity), and a measure of site contribution to gamma diversity. I hypothesised that using multiple diversity indices would add more insight into butterfly responses to disturbance than using a single diversity measure. I then aimed to compare how the results obtained using these measures were affected by including species similarity in the diversity calculation. I hypothesised that when species similarity was considered, the diversity patterns would be different to those found with the naïve indices and there would be less difference between sites. Finally, I aimed to explore how light-loving and canopy species influenced the observed diversity patterns. I hypothesised that in the open habitats of the most disturbed sites many light-loving species might be detected that would not be captured in our less disturbed forest understorey. If these species were present in the undisturbed forest, they would likely be found high in the canopy or in tree-fall gaps and forest edges.

5.3 Methods

5.3.1 Study design

Data were collected from 18 sites across a gradient of disturbance in the Manu region of south-east Peru, in a stratified sampling design. The gradient covered six different land uses, from minimally disturbed tropical forest to banana monoculture plantations. These land uses were ranked from highest to lowest disturbance intensity, with 1 being the most disturbed, as described in Chapter 2.

5.3.2 Data Collection

Butterflies were collected from each of the 18 sites across the disturbance gradient. I used two Van Someran traps at each site, one baited with rotten banana, and the other with fermented fish (Whitworth *et al*. 2018). The traps were located approximately 5m apart near the centre of the sites, hung so that the bottom of the trap was 1m above the ground, with a 5cm gap for butterflies to enter the trap. The traps were checked and rebaited daily and all butterflies caught were identified in the field using a photographic guide to local species compiled by the Crees Foundation, checked by a local entomologist and used for previous research in the area (Whitworth *et al*. 2016c, 2018). Butterflies were marked with a metallic Sharpie pen so that recaptures could be identified, but none were recaptured. Sampling was conducted over three weeks in September 2015, and three weeks in October 2016. Butterfly communities can show seasonal variation (Grøtan *et al*. 2014), so sampling was restricted to the end of the dry season to minimise any seasonal effects. Six sites were sampled each week, including one site of each disturbance level to control for the effects of weather. A total of ten days of trapping were conducted at each site, split evenly between the two years.

Because the highly disturbed habitats had very low canopy, I was restricted to using low traps only, as I wanted the trapping method to be consistent across the gradient. However, I know that some forest butterfly species are found only at high levels of the canopy, possibly because of the higher light levels (DeVries 1988; Whitworth *et al*. 2016c; Fauset *et al*. 2017), and so might not be detected using low traps. To explore how light-loving and canopy species influenced the

observed diversity patterns, two different options were used. First, I identified the species that seemed to show a strong preference for the disturbed habitats and reviewed the literature to identify those known to be light-loving species (Table S5.6) and excluded these from the data for comparison with the complete dataset. There was a risk that this approach could have disproportionately penalised the highly disturbed habitats, so a second approach was also used to explore what might have been captured had be sampled from the understorey to the canopy. This was possible because butterflies have been part of a long term monitoring project carried out at the MLC by the Crees Foundation. Data have been collected on the butterfly communities found in the different disturbance types within the MLC reserve, sampled using low, medium and high canopy traps (Whitworth *et al*. 2016c). These different disturbance types are the same forest areas as I have used as the least disturbed sites (ranks 4-6) in my study. The traps used by Whitworth *et al*. (2016c) were set up in April 2013 and ran until March 2014, with a total of 720 trap days per disturbance category. A total of 5219 individuals were captured, and 229 species. I used the data collected from the mid (15m) and high level (30m) traps, from the sites that were within my three least disturbed habitats (ranks 4-6). For each of the sites, I generated a dataset such as might have been obtained had I used high traps in my study. To do this, I took a random sample of the data from the MLC high/mid-level trap data (half the sample size of the data obtained in this study) and combined this with a random sample of 50% of the data from my low-level traps. This resulted in a generated dataset of the same sample size for each site as my original dataset but containing butterflies from all vertical strata.

5.3.3 Analysis

Butterflies were identified to species level (when species identification to a Latin name was not possible, morphospecies were used – we took photographs of the specimens and assigned them a numeric code, so that if more specimens of that type were found, they would receive the same identification), and classified by family, subfamily, tribe and genus. A taxonomic similarity matrix was created scoring each butterfly according to its similarity to other species. The similarity scores were adapted from the approach used by Shimatani (2001), with a score of 1 allocated for two individuals of the same species, 0.8 for different species in the same genus, 0.6 for the same tribe, 0.4 for the same subfamily, and 0.2 for the same family, and 0 for different families.

R version 3.3.2 (R Core Team 2017) and RStudio version 1.0.136 (RStudio Team 2016) were used for all analyses. Diversity was calculated using the package rdiversity v.0.4.3 (Mitchell & Reeve 2016), which calculates a range of indices based on Hill numbers (Hill 1973). These diversity indices have been developed for use at both the subcommunity level, which is the community found within a site (e.g. the community of butterflies found within one banana plantation), and at the metacommunity level, which consists of all the sites within the study system (the complete community of butterflies found over all 18 sites across the disturbance gradient). For these indices, q provides a measure of conservativeness to the estimates of subcommunity alpha diversity and the subcommunity contribution to gamma diversity, placing increasing importance on common species as q increases. For the beta diversity measures, increasing q places greater weight on the species that are more common in the subcommunity than the metacommunity (the least redundant). Each measure focuses on rarity at a different scale: in the case of alpha diversity, the emphasis is on species that are locally common in the subcommunity, for gamma, those that are globally common in the metacommunity, and for beta diversity the species that are relatively common at the subcommunity level compared to the metacommunity. Each index can be calculated naïve (all species treated as equally distinct) or using a similarity matrix to provide a similarity-sensitive measure of diversity (Reeve *et al*. 2016). I calculated alpha diversity ($\overline{\alpha}$), two measures of beta diversity (redundancy (ρ) and

representativeness ($\overline{\rho}$), and gamma diversity (γ) for each site at q = 0, 1, 2 and ∞, both with and without accounting for species similarity.

I calculated the estimated alpha diversity at equal sample sizes (n = 280), using iNEXT v.2.0.14 (Hsieh, Ma & Chao 2016) with the abundance sensitive formula, 40 knots and bootstrapped 100 times. I also calculated the sample coverage, extrapolating up to a sample size of 300 for each site (Figure S5.1).

I used Spearman rank correlation tests (Spearman 1904) to compare the patterns of diversity with disturbance rank, as this makes no assumptions about the underlying distribution of the data. To assess the overall response of each index to human disturbance across multiple values of q, a permutation test (10,000 permutations) was used to obtain the combined p-value of each index ($\overline{\alpha}$, ρ, $\overline{\rho}$ and γ) at q = 0, 0.5, 1, 2 and ∞. Because q = 1 (Shannon diversity) provides a balance between over-weighting either dominant or rare species, I included q = 0.5 to provide a balance against q = 2 to avoid under-weighting of rare species when calculating the overall pattern of alpha diversity across multiple values of q. General linear models were also used to check that elevation rainfall and distance to the river had no significant effect on the relationship between diversity and disturbance for the sites in order to control for them as necessary. All three of these variables were included in the models for each of the biodiversity response variables (abundance, and alpha, redundancy, representativeness and gamma contribution at each q) and Moran's I test was used to check for spatial autocorrelation in the residuals of the models.

The analyses above were repeated using the two alternative datasets generated: the data with known light-loving species excluded, and the dataset incorporating data from mid and high canopy traps collected in the previous study by Whitworth (2016c). These results of these were compared with the results using the original data to see if they could help explain some of the patterns found. I used visual comparisons of the diversity profiles along with paired-t-tests to determine how the diversity of the original data compared with the generated datasets. For these comparisons, the less disturbed sites (ranks 4-6) were grouped together, and the more disturbed (ranks 1-3) grouped, as the nature of the generated datasets meant I expected the more and less disturbed sites to

show opposite responses compared to the original data. Spearman rank correlation tests were used to test if the strength of the correlation between diversity and disturbance changed when using the generated datasets in place of the original data. Using these two generated datasets to compare with my original collected data provided further insights into what my main results could tell me about how butterfly diversity changes across a gradient of human disturbance.

5.4 Results

A total of 2506 individuals of 257 species were collected (listed in Table S5.1), of which 59 couldn't be identified and were assigned morphospecies numbers and 13 that comprised individuals that escaped or were too worn to be identified beyond genus or higher levels. The sample completeness curves suggest that we had captured around 90% of species at most sites, but for a few of the disturbed sites where butterfly abundance was lower, further sampling would have been desirable (Figure S5.1). There is some degree of mimicry present in Neotropical butterflies, so extra care was taken in the identification of groups where mimicry was known to be high, such as *Heliconius*, and advice on what to check was obtained from a local lepidopterist to minimise the risk of species misidentification, though this could not be eliminated entirely. The full results of all correlations tests and linear models can be found in the supplementary materials (Tables S5.2, S5.3, S5.4 and S5.4).

5.4.1 Alpha diversity

There was no significant correlation between overall alpha diversity ($\overline{\alpha}$) and disturbance rank. This was true for both the naïve measures and the similarity-sensitive alpha diversity measures (permuted combined p-value for q = 0, 0.5, 1, 2, and ∞: naïve p = 0.051, similarity-sensitive p = 0.073). When alpha diversity was estimated at equal sample sizes using iNEXT, there was also no significant correlation with disturbance rank (permuted combined p-value for q = 0, 0.5, 1 and 2: p = 0.596; p > 0.2 at all individual values of q).

Naïve species richness (q = 0) was higher in the less disturbed forest (rho = 0.635, p = 0.005, Figure 5.1a) than in the more disturbed sites. However, the

reverse pattern emerged once the taxonomic similarity of species was accounted for (Figure 5.1b), although this was non-significant and fairly weak (rho = -0.266, p = 0.285). The difference between the naïve and similarity-sensitive results indicates that a greater diversity of higher taxonomic levels (e.g. more subfamilies) are found in the more disturbed forest. At higher values of q, the difference in naïve species diversity between sites is greatly reduced; from this I deduce that most of the extra species found in the less disturbed sites are rare, as even at q = 1, although there is a similar trend the correlation between diversity and disturbance is no longer significant (rho = 0.404, p = 0.09). When taxonomic similarity is considered, the correlation between alpha diversity and disturbance remains as q increases, with a high correlation at q = 1 (rho = -0.47, p = 0.04) and a trend at q = 2 (rho = -0.455, p = 0.058). This is because most families, subfamilies and tribes are well represented, even though rarity is common at the species level.

At q = 0, rare species and common species contribute equally to the diversity of a site and as q increases, the dominant species carry more weight. This means that the gradient of the relationship between effective alpha diversity and q indicates the evenness of the community at each site (the smaller the slope, the more even the community). The more disturbed sites generally have more even communities than the less disturbed sites (Figure 5.1a), which have many rare species resulting in a steeper gradient. When species similarity is considered (Figure 5.1b), there is much less difference in evenness between the sites, as there is little variation in the relative abundances of the higher taxonomic levels between sites.

The Moran's I test for spatial autocorrelation indicated potential spatial autocorrelation in the residuals of the model of naïve alpha diversity at q = 0 and q = 1, and redundancy at q = 1 (Table S5.4). To check that the described patterns were real, the linear models were re-run including the spatial coordinates. For the naïve alpha diversity models, the latitudinal coordinates were responsible for much of the autocorrelation, but for redundancy it was the longitudinal coordinates. For naïve alpha diversity at q = 0 and redundancy at q = 1, disturbance rank was still a significant explanatory variable when the latitudinal coordinates were included (Table S5.3), but the effect of disturbance on alpha diversity q = 1 was no longer clear, nor on redundancy when the

longitudinal coordinates were included. However, this pattern did not emerge in any of the other models tested, and together with the weakness of the autocorrelation and the suggested autocorrelation happening in different directions for related measures, there was little evidence that this was an important effect.

When light-loving species were removed, and similarity-sensitive alpha diversity recalculated, the pattern of alpha diversity across the gradient changed (supplementary materials Figure S5.2b). In the original dataset (Figure S5.2a), the more disturbed sites had higher similarity-sensitive alpha diversity than the less disturbed sites, because a wider range of higher taxonomic levels (e.g. genus, tribe) were represented here, quite possibly genera or subfamilies of light-loving butterflies. This hypothesis was supported as there was no correlation between similarity-sensitive alpha diversity and disturbance rank once the light-loving species were removed from the data (Spearman rank correlation: rho = 0.15, p = 0.536; Figure S5.2b). When I combined my data with the additional canopy trap samples, the pattern observed in the original data was completely obscured, with the less disturbed sites now having comparable similarity-sensitive alpha diversity to the more disturbed sites (Spearman rank correlation: rho = -0.03, p = 0.891; Figure S5.2c). As well as detecting light-loving species in the canopy, these patterns could also be partly due to the detection of undisturbed forest canopy specialist species that were not found in the more disturbed sites, including some previously undetected genera. It is also possible some of these additional species may be seasonal, as the canopy trap data were collected throughout the year, whereas my samples were only collected in September-October and neotropical butterfly communities have been found to vary between wet and dry seasons (Grøtan *et al*. 2012).

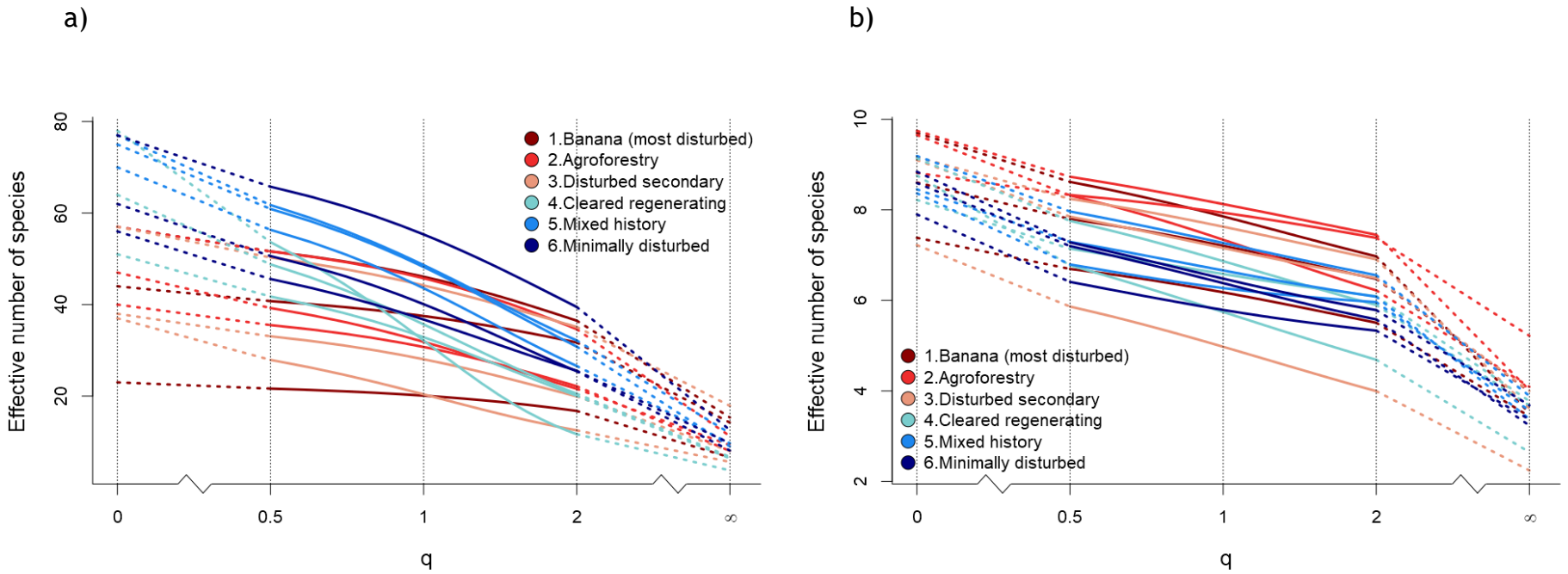

Figure 5.1 Alpha diversity across the disturbance gradient (a) in the naïve case, where all species are equally distinct, and (b) when taxonomic similarity of the species has been incorporated into the diversity measure. The disturbance rank is represented by a gradient of colours going from dark red for the most disturbed sites (banana plantations) to dark blue for the least disturbed (minimally disturbed forest). The relative contribution of rare species to the diversity of a site is indicated by q (on a log scale); at q = 0, rare and common species contribute equally to the diversity (species richness), whereas at q = ∞, only the most dominant species count (Berger-Parker index). The relationship between alpha diversity and disturbance changes depending on the value of q and whether naïve diversity (q = 0: rho = 0.63 , p = 0.005; q = 1: rho = 0.40, p = 0.10; q = 2, rho = 0.10, p = 0.70; q = ∞; rho = -0.04, p = 0.86) or similarity-sensitive diversity (q = 0: rho = -0.27, p = 0.28; q = 1: rho = -0.48, p = 0.04; q = 2, rho = -0.45, p = 0.06; q = ∞,; rho = -0.38, p = 0.12) is considered. Solid lines indicate where diversity was calculates at intervals of q = 0.1, whereas for the dashed lines diversity was calculated only at the start and end of the dashed sections.

5.4.2 Beta diversity

Overall, as disturbance intensity increased, the sites had a higher naïve redundancy (ρ) (permuted combined p-value for q = 0, 0.5, 1 and 2: $p < 0.001$ ($q = \infty$ was excluded as all sites converged to a value of 1 as q approached ∞, since all sites had at least one unique species). Similarity-sensitive redundancy also increased with increased disturbance (permuted combined p-value for q = 0, 0.5, 1, 2 and ∞: $p < 0.001$). When each value of q was considered independently, there was a significant correlation between naïve redundancy and disturbance rank at q = 0 (rho = -0.787, $p < 0.001$) and q = 1 (rho = -0.661, $p < 0.002$), but not at q = 2 (rho = -0.216, $p = 0.388$; Figure 5.2a). Similarity-sensitive redundancy correlated strongly with disturbance rank at q = 0, 1 and 2 (rho < -0.79, $p < 0.001$ for all; Figure 5.2b), but not at $q = \infty$. This suggests that should one of the more disturbed sites be lost, comparable communities could be found elsewhere in the study region. However, if a low disturbance site was lost there is a greater risk of that butterfly community disappearing entirely. The same is true for the similarity-sensitive redundancy results — the more disturbed sites have highly redundant butterfly communities, because you could go almost anywhere else in the metacommunity and find the same families and subfamilies that you get in the highly disturbed sites, in similar relative abundances. The low disturbance sites have low redundancy, suggesting that they hold butterfly communities with tribes or subfamilies that might be rare elsewhere in the metacommunity; the overall sizes of the low-disturbance communities are also bigger (rho = 0.8029, $p < 0.001$), which also contributes to their low redundancy in the metacommunity.

As q increases, the difference in naïve redundancy between the sites quickly narrows, but with the similarity-sensitive redundancy measure, a strong correlation persists up until $q = \infty$. As q increases, the redundancy index focuses on the least redundant species found in the site. At $q = \infty$, the naïve redundancy converges at 1, which indicates that there is at least one rare, unshared species found in each site. The similarity-sensitive redundancy did not converge at 1, as the higher taxonomic levels were found across multiple sites.

When the canopy data were combined with the low-trap data, the naïve redundancy of the less disturbed sites became higher than the more disturbed

sites (Spearman rank correlation: rho = 0.80, $p < 0.001$; Figure S5.5c). This did not happen when light-loving species were excluded (Spearman rank correlation: rho = -0.78, $p = 0.001$; Figure S5.5b). It was necessary to combine data from multiple canopy traps to obtain a sufficient sample size of canopy data to combine with the low-trap data. Therefore, the canopy samples of the sites within a disturbance category are likely to be more similar to each other than if each site was represented by a distinct canopy trap. This is a possible reason for the higher redundancy of these sites, an artefact of my resampling approach. It is, however, also possible that this is a real effect and that within low-disturbance forest, species are widespread, as a broad range of resources are available throughout this habitat type. To determine this, it would be necessary to compare data collected from high traps at multiple sites within the same forest type to determine the amount of variation between sites.

a)

b)

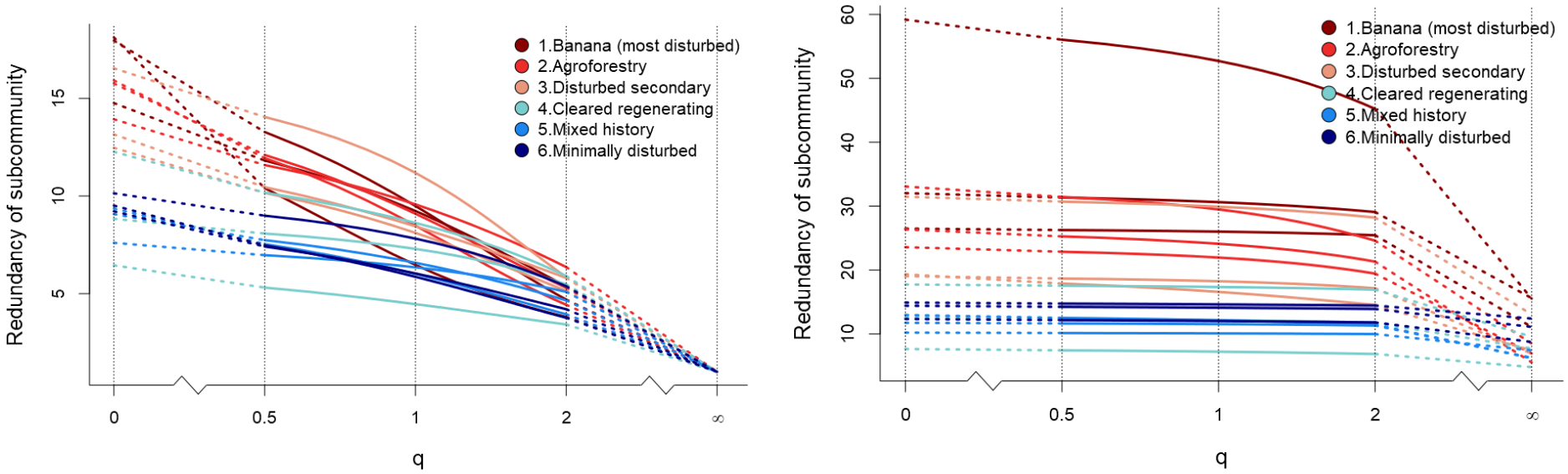

Figure 5.2 Redundancy of the communities across the disturbance gradient (a) in the naïve case, where all species are equally distinct, and (b) including the taxonomic similarity of the species. The disturbance rank is represented by a gradient of colours going from dark red for the most disturbed sites (banana plantations) to dark blue for the least disturbed (minimally disturbed forest). Increasing values of q on the x-axis represent increasing conservatism in the estimate of redundancy. The relationship between redundancy and disturbance changes depending on the value of q and whether naïve diversity ($q = 0$: $rho = -0.79$, $p < 0.01$; $q = 1$: $rho = -0.66$, $p < 0.01$; $q = 2$, $rho = -0.22$, $p = 0.39$) or similarity-sensitive diversity ($q = 0$: $rho = -0.81$, $p < 0.01$; $q = 1$: $rho = -0.81$, $p < 0.01$; $q = 2$, $rho = -0.80$, $p < 0.01$; $q = \infty$, $rho = -0.19$, $p = 0.45$) are considered. Solid lines indicate where diversity was calculates at intervals of $q = 0.1$, whereas for the dashed lines diversity was calculated only at the start and end of the dashed sections.

Redundancy is influenced by the abundance of individuals in the subcommunity; to control for differences in the sizes of the subcommunities I also looked at the representativeness ($\overline{\rho}$) of the sites. Disturbance rank was strongly correlated with how representative ($\overline{\rho}$) the sites were of the metacommunity. For the same population size, representativeness is directly correlated with redundancy; in my data, the effect of the difference in population size between the sites was so strong that not only did it cancel out the differences between sites, it reversed the pattern observed. Less disturbed sites were more representative of the metacommunity than the heavily disturbed sites. This was true for both the naïve representativeness (permuted combined p-value for q = 0, 0.5, 1, 2 and ∞: p = 0.009, Figure 5.3a), and the similarity-sensitive representativeness (permuted combined p-value for q = 0, 0.5,1,2 and ∞: similarity-sensitive p < 0.001, Figure 5.3b). Individually, there was a strong positive correlation between naïve representativeness at each value of q (0,1,2 and ∞) and disturbance rank (rho > 0.73, p < 0.001 for all). When representativeness accounted for species similarity, there was no significant correlation with disturbance rank at q = 0 (rho = 0.053, p = 0.834), but the strength of the correlation increased with increasing values of q (at q = 1, rho = 0.423, p = 0.08), and was significant at q = 2 (rho = 0.593, p = 0.009) and q = ∞ (rho = 0.831, p < 0.001). The higher representativeness of the less disturbed sites suggests that they hold a larger proportion of the total number of species present in the ecosystem. The abundance and richness of a site, as well as the species composition, may influence the redundancy and representativeness of the sites. More individuals were found in the less disturbed sites, which increases the chance of any one species being present in that sample, thereby making it more representative. However, it is also likely that the less disturbed sites are home to resources that are scarce elsewhere, allowing them to support species that cannot persist in more disturbed habitats.

I found little change in the naïve representativeness when light-loving species were excluded, since the less disturbed sites are relatively successful at representing the other species found across the gradient (Figure S5.3b). A stronger effect was seen when I combined the extra canopy data with my low-level trap data — the naïve representativeness of the most disturbed sites decreased (paired t-test (8 df): t = 6.73, p = 0.0001, mean-difference = 0.13)

whilst that of the less disturbed sites remained unchanged (paired t-test (8 df): t = 1.02, p = 0.34, mean-difference = 0.02), resulting in a larger separation between the more and less disturbed habitats (Figure S5.3c). This is likely to be because the less disturbed sites now included many of the light-loving species found in the canopy, as well as additional forest canopy specialists absent from the most disturbed sites, which the more disturbed sites were unable to represent.

There was no change in the similarity-sensitive representativeness ($\overline{\rho}$) of the more disturbed sites when the light loving species were removed from the data (paired t-test (8 df) at q = 1: t = -2.27, p = 0.05, mean-difference = -0.02; Figure S5.4b). However, when the canopy data were incorporated, the similarity-sensitive representativeness of the least disturbed sites increased slightly (paired t-test (8 df) at q = 1: t = -3.10, p = 0.015, mean-difference = -0.02) and the variation between the sites decreased (Figure S5.4c). The mean similarity-sensitive representativeness of the more disturbed sites remained constant, but again the variation was reduced (Figure S5.4c). This resulted in a stronger correlation between similarity-sensitive representativeness and disturbance rank (Spearman rank correlation: rho = 0.87, p < 0.001). This suggests that the canopy does contain many of the light-loving species previously not detected in the forest understorey, but also contains some species not found in the more disturbed sites. However, at q = ∞, the sites become more similar than they were in the original data, suggesting that the additional species found in the less disturbed sites have low redundancy, whereas the species previously associated with the high-disturbance sites (e.g. some of the light-loving species) were now more redundant, as they could be detected in the canopy of the less-disturbed forest.

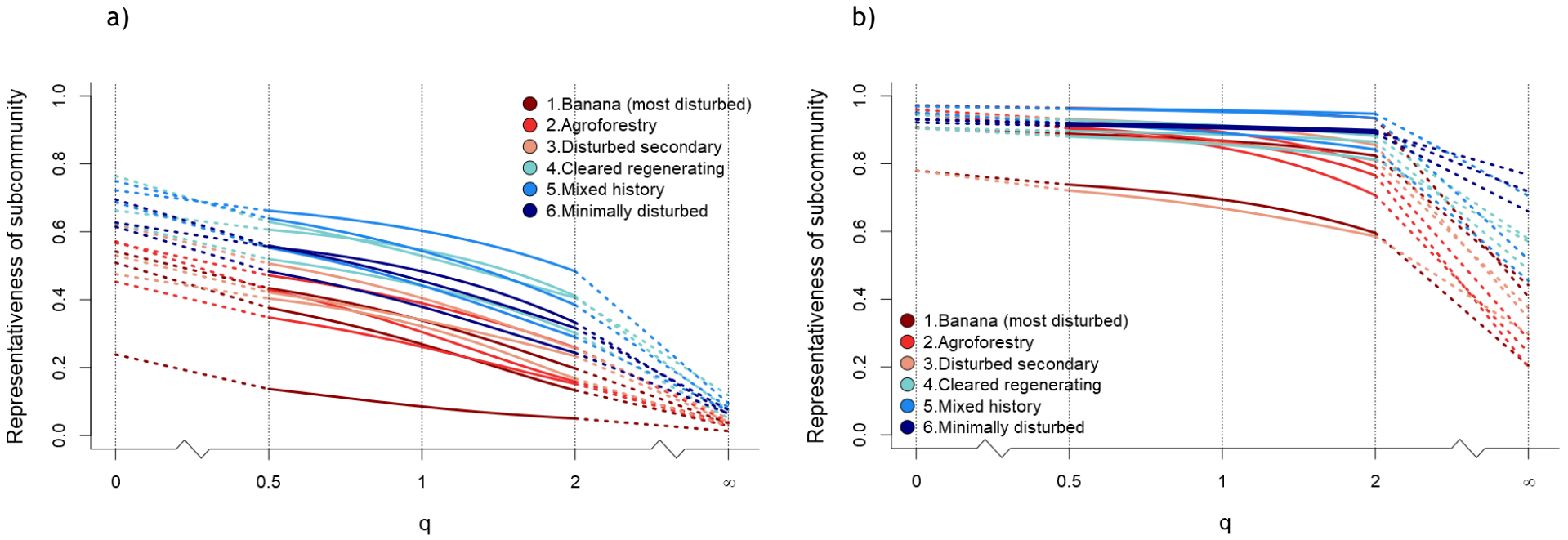

Figure 5.3 Representativeness of the sites across the disturbance gradient in (a) the naïve case and (b) incorporating similarity into the measure. Representativeness ($\bar{\rho}$) is a measure of how well an individual site represents the whole metacommunity (all sites combined). The disturbance rank is represented by a gradient of colours going from dark red for the most disturbed sites (banana plantations) to dark blue for the least disturbed (minimally disturbed forest). Increasing values of q on the x-axis represent increasing conservatism in the estimate of representativeness. The relationship between representativeness and disturbance changes depending on the value of q and whether naïve diversity (q = 0: rho = 0.75 , $p < 0.01$; q = 1: rho = 0.75, $p < 0.01$; q = 2, rho = 0.74, p = < 0.01; q = ∞; rho = -0.80, $p < 0.01$) or similarity-sensitive diversity (q = 0: rho = 0.05, p = 0.83; q = 1: rho = 0.42, p = 0.08; q = 2, rho = 0.59, $p < 0.01$; q = ∞, rho = 0.83, $p < 0.01$) are considered. Solid lines indicate where diversity was calculates at intervals of q = 0.1, whereas for the dashed lines diversity was calculated only at the start and end of the dashed sections.

5.4.3 Gamma diversity

Contribution per butterfly to overall naïve gamma diversity (γ) increased with increased disturbance intensity (combined permuted p-value at $q = 0, 0.5, 1, 2$ and ∞: $p = 0.042$; Figure 5.4a). The correlation of disturbance rank with naïve gamma diversity at $q = 0$, 1 and 2 independently was moderately strong ($rho < -0.4$ for all), although $0.05 < p < 0.1$ when each value of q was considered independently. The higher γ of the more disturbed sites means that each individual found at that site contributes relatively more to the total diversity of the metapopulation (the whole gradient) compared to the less disturbed sites. This is partly due to the differences in sample size, with fewer butterflies being detected in the more disturbed sites, and that some of these species may be uncommon in less disturbed sites, so these unusual species mean that the high disturbance sites can add more diversity than expected for their small size. So because of the small number of individuals, and the fact that many of these are rare across the gradient as a whole, each individual detected in the most disturbed sites adds a lot of diversity to the overall gradient relative to the number caught at the site.

When species similarity is considered, the difference in gamma diversity contribution across the gradient becomes more pronounced (Figure 5.4b). The most disturbed sites have significantly higher γ than the less disturbed sites overall (combined permuted p-value at $q = 0, 0.5, 1, 2$ and ∞: $p < 0.001$), and when I examined the correlation between disturbance rank and γ at $q = 0$, 1 and 2 independently, I found a very strong correlation ($rho < -0.75$, $p < 0.001$ in each case). From this, I deduce that the most disturbed subcommunities are contributing individuals from tribes or families that are uncommon across the rest of the gradient, and therefore contribute more to the overall gamma diversity of the metacommunity. This was contrary to my expectation that less disturbed forest would be likely to contribute more to the overall gamma diversity of the metacommunity, but these findings are consistent with the low representativeness of the more disturbed sites seen in Figure 5.3, and may be driven by open-habitat species that prefer bright, open spaces, and whilst these are common in the most disturbed areas, they may be rare in the gradient as a whole.

Removing the light-loving species reduced the naïve gamma diversity contributions of the most disturbed sites (paired t-test (8 df): t = 4.43, p = 0.002, mean-difference = 8.06; Figure S5.6b), suggesting that these are the species that these sites add to the metacommunities. However, combining the canopy data did not produce the same result (Figure S5.6c), as the gamma contributions of the most disturbed sites actually increased (paired t-test (8 df): t = -13.71, p = <0.001, mean-difference = -79.26), suggesting there are some light-loving species found in the disturbed habitats that the forest data are still not capturing even when including the canopy.

Finally, when I look at the similarity-sensitive gamma diversity contribution (Figure S5.7), I find further evidence to support the hypothesis that the main driver for the high gamma contribution of the more disturbed sites was a result of light-loving species not being well sampled in the less disturbed forest. Once the light-loving species were excluded from the data, there was no discernible difference across disturbance ranks in their contribution to metacommunity gamma diversity per individual sampled (Spearman rank correlation: rho = -0.35, p = 0.149; Figure S5.7b). The same pattern occurred when the canopy samples were included (Spearman rank correlation: rho = -0.44, p = 0.06; Figure S5.7c), suggesting that the light-loving species and genera found previously in the more disturbed sites were now detected across the whole gradient, so the contributions of the more disturbed sites were no longer as important a contribution to the metacommunity as they had been in the original dataset.

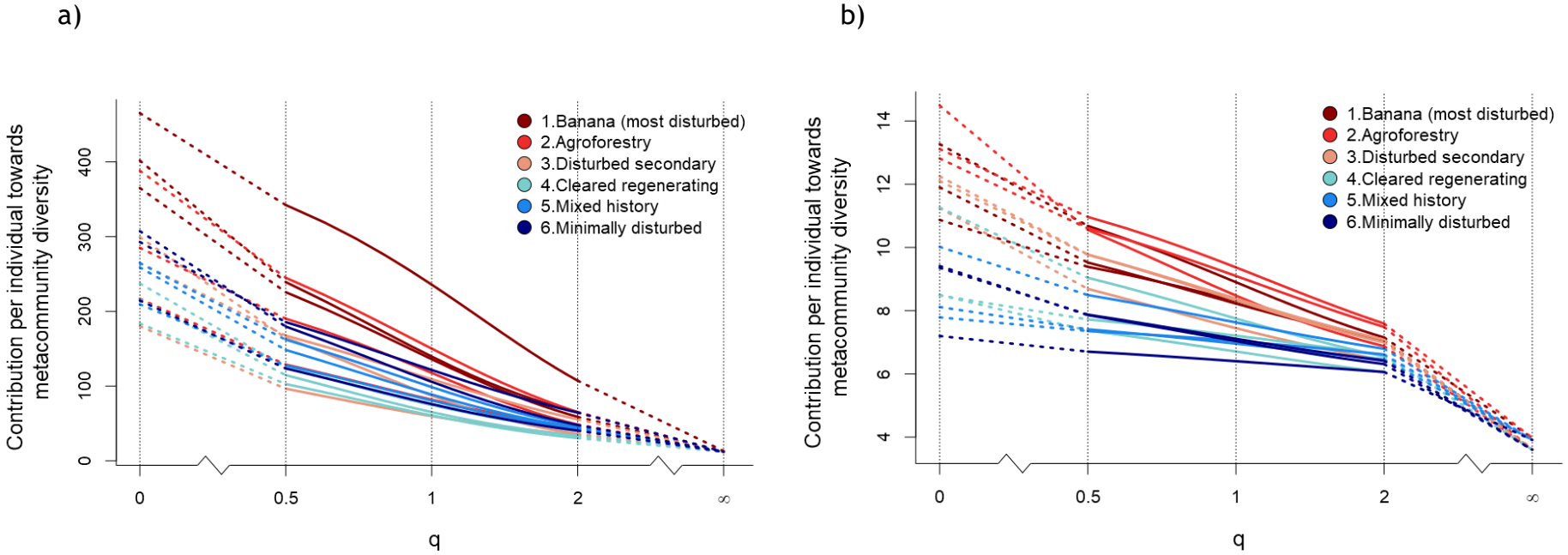

Figure 5.4 Contribution of each site to the gamma diversity of the metacommunity (a) in the naive case and (b) when taxonomic similarity of the species has been incorporated into the diversity measure. This subcommunity index of gamma diversity is a measure of how much each site contributes to the gamma diversity of the whole metacommunity (all sites sampled) per individual encountered at that site. The colours indicate the disturbance level of the site, with dark red representing the most disturbed (banana plantations) and dark blue the least disturbed (minimally disturbed forest). Along the x-axis, q indicates the relative importance of rare species, with rare species contributing less as q increases. The relationship between disturbance and the contribution to gamma diversity changes depending on the value of q and whether naïve diversity (q = 0: rho = -0.47 , p =0.05; q = 1: rho = -0.45, p =0.06; q = 2, rho = -0.41, p = 0.09) or similarity-sensitive diversity (q = 0: rho = -0.77, p < 0.01; q = 1: rho = -0.80, p < 0.01; q = 2, rho = -0.78, p < 0.01) are considered. Solid lines indicate where diversity was calculates at intervals of q = 0.1, whereas for the dashed lines diversity was calculated only at the start and end of the dashed sections.

5.5 Discussion

Using multiple approaches to butterfly diversity measurement added valuable information to our understanding of biodiversity patterns along a disturbance gradient in ways that could help inform conservation priorities and monitoring. Butterflies responded negatively to disturbance along a gradient of human land-use intensity in southeast Peru. Both alpha and beta diversity were important for detecting the responses of the community, and my results suggest neither is sufficient on its own to understand biodiversity responses to disturbance. Rare species were more sensitive to disturbance, with species richness being the most sensitive measure of alpha diversity change across the gradient. Tropical forests are well known for holding a high proportion of rare species, of butterflies and other taxa (DeVries, Murray & Lande 1997; Novotný & Basset 2000), so it is unsurprising that they make an important contribution to the diversity patterns detected. Community composition also changed in response to disturbance, with the redundancy of the communities increasing in more disturbed habitats, and fewer light-loving species detected in the less-disturbed forest, supporting the recommendation by Stork *et al.* (2017) that it is important to consider changes in community composition as well as richness. Incorporating species similarity into the diversity measures led to some opposing patterns being detected across the gradient compared to the naïve measures, demonstrating how species identity and relatedness may be key factors to consider in conservation assessments. My results indicate that simple solutions to the problem of how to quantify biodiversity changes, such as the use of species richness on its own, are insufficient to understand the true impacts of disturbance. Rather, what my results highlight is that biodiversity patterns are complex, and that there are many subtle parts to the story that are at risk of being overlooked if the assessment is oversimplified, which is in agreement with several other recent publications (Santini *et al.* 2017; Veach *et al.* 2017; Moreno *et al.* 2018). However, as well as demonstrating the importance of using multiple measures, as in these other works, my study also addresses two other major challenges in biodiversity assessments: firstly, the measures I have chosen are all part of a mathematically cohesive family, overcoming the issue of using multiple diversity indices that are not directly related to one another; secondly, I have demonstrated how similarity sensitive diversity measures can be applied to

account for the fact that not all butterfly species are equally distinct from one another, which has before now been almost entirely overlooked in tropical forest biodiversity studies. Overall, I found that using a combination of diversity measures enabled a much more detailed understanding of biodiversity responses to environmental change. This approach can be easily incorporated into biodiversity studies, along with a consideration of multiple taxa and/or functional groups, to provide more comprehensive evidence for conservation strategy.

Butterflies declined in abundance and species richness in response to disturbance in this study, which is consistent with several previous studies (Barlow *et al*. 2007b; Stork *et al*. 2017). However, other studies suggest that the response patterns of this group could vary widely, with butterfly communities sometimes found to thrive in high quality forest, and other times in fragmented, open and mosaic habitats (Cleary 2004; Kudavidanage *et al*. 2012). Therefore, one must be wary of assuming high butterfly richness is correlated with low forest disturbance in other regions, or of using richness on its own as an indication of high-quality habitat or a sole target for conservation efforts (Veach *et al*. 2017). The mixed responses of butterflies, with occasional increases in diversity with increased disturbance (Kudavidanage *et al*. 2012), could hypothetically be used to recommend disturbed habitats as priorities for conservation if species identities and other taxa are not considered. However, many of the species found in these disturbed habitats probably still require large areas of primary forest in the vicinity in order to persist (DeVries, Murray & Lande 1997), and may not be equal in conservation value (Spitzer *et al*. 1997), with forest specialists struggling to cross agricultural landscapes if suitable habitats and host plants are unavailable (Scriven *et al*. 2017). The decline in abundance in the more disturbed sites meant that sampling completeness was also lower, particularly in the banana plantations. Increased sampling effort to reach near-complete coverage at all sites would have been ideal, but I would not expect this to dramatically change the results, as the alpha diversity and representativeness measures are normalised in order to account for the differences in the sizes of the subcommunities, assuming equal sampling effort. The redundancy and contribution to gamma diversity measures are sensitive to the number of individuals, but this information is useful for understanding the

contributions of individuals to the diversity of the site and region. For this reason, using these indices together is optimal for understanding changes in biodiversity patterns.

It is often not clear what a project is aiming to achieve by using butterflies as indicators for conservation management, as maximising butterfly richness, for example, could hypothetically result in management strategies that are damaging for the forest dependent taxa, which are generally more vulnerable, and provide important ecosystem services (Bradshaw, Sodhi & Brook 2009). In order to assess how disturbance or regeneration of a tropical forest is impacting biodiversity and/or ecosystem functions, it is important to assess a broad range of taxonomic groups before drawing any conclusions on what is the best management strategy for conservation, or threshold of disturbance to be avoided (Lawton *et al*. 1998). Of course, the more taxa to be surveyed, the more resources are required, so careful selection of a group of taxa that are efficient to sample and show sensitive responses to disturbance (indicator taxa) is a sensible approach. But ideally, these should include several groups with different resource requirements that encompass a range of roles in forest processes. The additional effort and resources required to study multiple taxa are small in relation to the cost of setting up a field-based study, and so is a worthwhile additional investment where possible, and study groups can be chosen based on their survey efficiency (Gardner *et al*. 2008a).

Including species-similarity in the quantification of biodiversity is an important step forward, as it enables us to acknowledge the importance of the relationship between species present in the ecosystem. High genetic, taxonomic and functional diversity are important for ensuring communities can maintain ecosystem resilience and function, and adapt to changing environments (Hooper *et al*. 2005; Moreno *et al*. 2018). For example, in the case of butterflies, high functional diversity may mean that caterpillar herbivory is spread across a range of plant species, and if functional diversity is reduced, the herbivory may increase for a small number of plant species, whilst others experience a release, resulting in a change in vegetation composition that could affect the resources available to other animals. A combination of increased herbivory and decreased pollination of some plants could push the ecosystem to an increasingly vulnerable state and reduce its resilience because the levels of functioning are

not high enough to enable rapid recovery following environmental disturbances, such as landslides. In this study, I found that the inclusion of similarity in the diversity calculations resulted in very different patterns to the naïve measures, sometimes even showing a reverse trend, such as in Figure 5.1. This is likely to be because open habitat and light-loving species are found in the more disturbed habitats, belonging to genera and tribes not encountered frequently in the forest understorey, but some of these may be present in the forest canopy, as demonstrated in the analyses excluding known light-loving species and combining data from high canopy traps. It would be interested to see how these patterns might compare if functional similarity was used in place of taxonomic similarity, but there is limited functional data available for neotropical butterflies so it is difficult to predict what the outcome might be.

Using a similarity sensitive approach may provide greater robustness in the face of uncertain species identification – this is particularly useful for groups, such as *Heliconius,* where mimicry is known to be common (Sheppard *et al*. 1985) or for cryptic species. If two individuals of the same genus are mistakenly identified as the same species, then the similarity scores mean the effect of this on the diversity values would be minimal; their contribution to the diversity would be 1 instead of 0.8, rather than 1 or 0 using a traditional approach. The similarity-sensitive measures discussed in this study can help us include these components in our assessment and comparison of site diversity. Ideally, the similarity scores would be based on some quantifiable measure, such as genetic similarity or morphology to create the species similarity matrix. The best option for assessing similarity will depend on both your question of interest as well as the data available. In this case, as I was interested in taxonomic similarity, evolutionary distances could have been used to inform the relative differences between genera, subfamily and family levels. Unfortunately, I was unable to find enough information on this, so I used equally distributed similarity scores based on those used by Shimatani (2001), which assumed that the difference between genera was half the difference between tribes, and so on (see methods). To check the sensitivity of the results to these values, I did explore alternative scoring systems for creating the similarity matrix and found only minor effects on the results. Exploring these options extensively and systematically was beyond the scope of this study, but this would warrant further investigation if this approach

were to be widely adopted. In studies where more information is available, I recommend the scores be adjusted accordingly. The other difficulty with choosing a suitable scoring system is that the similarity between species at each taxonomic level is not constant. For example, some genera are more closely related than others (Seraphim *et al*. 2018), which cannot be captured by the similarity matrix. This means there may be some subjectivity in the researcher's decision on what level of difference is of interest to the study, and then potentially using the mean similarity value for each level.

As well as avoiding drawing conclusions from a single taxon, it is important to note the importance of careful choice of biodiversity indices, ideally including a profile of diversity with varying emphasis of rare species to gain multiple perspectives. A spectrum of alpha diversity can quickly and easily be produced using Hill numbers, providing multiple perspectives on how communities change in response to the variable of interest. It is too common for the story to stop at alpha diversity, and this may fail to uncover important changes in communities (Hillebrand *et al*. 2017). In my case, if I had relied solely on estimated or observed Shannon or Simpson's diversity, for example, I would have wrongly concluded that there was no change in butterfly diversity in response to disturbance. For almost all purposes, the quality of the community is as important as the quantity of species, with different species providing different types and levels of ecosystem function, and threatened species often being of greater conservation concern than more common ones. If only alpha diversity is considered, then two communities with equal numbers of species in similar relative abundances would be considered of equal conservation value. However, it is possible that one of those communities is comprised of disturbance tolerant, widespread species, whilst the other contains specialist, range restricted species (Hamer *et al*. 2003). My results show how beta diversity measures can identify this species turnover component and highlight that the two communities are not as similar as they might seem using only alpha diversity.

From the gamma diversity analysis, I found that the individuals from the more disturbed sites were contributing more to the overall diversity of the region than those from the less disturbed sites, which was initially a counterintuitive result. The open habitat created by clearing land for banana plantations creates an environment with much more light, and there are many species of butterflies

known to be affiliated with sunny patches. Therefore, it is likely that some of the butterflies found in the banana plantations (and other more disturbed, brighter habitats) are species that are not found in the forest understorey because it is too dark. Many of these light-loving species are related, and fall within the same tribe or subfamily, which would also explain the results of the similarity-sensitive gamma diversity. When we removed the light loving species from the analysis, and when we incorporated additional canopy data, the differences in gamma diversity contributions were no longer detectable, lending additional support to this theory. Advances in biodiversity analysis have made it much more accessible and efficient to calculate multiple indices, with a range of packages and platforms available (Hsieh *et al*. 2016, Mitchell & Reeve 2016, Oksanen *et al*. 2017).

5.6 Conclusion

In this study, I have demonstrated how recent advances in diversity measurement can provide further insight into biodiversity responses to human disturbance and highlight the importance of critical selection of appropriate diversity measures for use in biodiversity and conservation research. Incorporating similarity-sensitivity into diversity measurement can radically change the patterns detected and this should be an important consideration, as similarity-sensitive diversity measures could help to capture features of high conservation relevance, though care should be taken to avoid overlooking closely-related rare species.

I found that butterflies show a negative response to increasing disturbance along the land-use gradient used in this study. As disturbance intensity increased, there was a loss in species richness, and an increase in the redundancy of the communities. I suggest it is important to use more than one measure of diversity, as important patterns can be easily overlooked if a single measure is chosen, whether it is broadly appropriate or not. Using multiple measures refers to both the use of several values of the parameter q to understand how rare species are influencing the diversity response, as well as a combination of alpha and beta diversity indices. The best measure for addressing a particular research question may depend on how much importance you place on rare species. However, using a spectrum of q values means that you can consider the response

of the community from multiple perspectives and understand the relative roles of both rare and dominant species in the communities and the evenness of those communities.

The alpha and beta components of diversity should both be considered because they add very different information to describe a community. I found that the newly developed measure of beta diversity known as redundancy (ρ), was particularly informative in the context of this study. Measuring redundancy allowed me to identify which sites would be hardest to replace if they were lost, and which sites might be of less relative value for conservation purposes.

I have demonstrated how species similarity can be incorporated into the diversity measures to detect how human disturbance affects the butterfly community, recognising that not all species are equally distinct. Very different patterns emerged depending on whether the similarity of species was accounted for or not. This is an important consideration depending on the goal of a project — is it to preserve genetic or taxonomic diversity, maximise the number of species present, or preserve high functional diversity to protect the resilience of ecosystem functions? Species similarity adds a valuable extra layer of information that can help to distinguish between areas of similar numbers of species based on other factors that may be important, such as the genetic, functional or taxonomic diversity each site holds. These may indeed be of greater importance for conservation purposes than simply the raw number of species.

6 Using soundscape diversity to assess the impacts of human disturbance on tropical forest biodiversity.

6.1 Abstract

Rainforest environments are challenging to survey, with many of their component organisms difficult to detect through traditional sampling methods, requiring extensive time and expertise. Acoustic survey methods can be useful for detecting sound-producing species from a broad range of taxonomic groups, and analysis using acoustic diversity indices can enable the acoustic community to be quantified without the need for identification of individual species. In this study, I used a soundscape approach to assess the change in the acoustic community along a gradient of human disturbance in the Amazon rainforest. My results indicated that the soundscape generally remains well preserved as disturbance intensity increases across the gradient. This may be because the soundscape of this region is dominated by insects, especially cicadas and Orthoptera, that may be relatively insensitive to disturbance, whereas species more sensitive to human disturbance may contribute less to the soundscape diversity. I also observed a decline in acoustic diversity at low disturbance, protected forest sites close to the research station. I suggest this may be indicating potential negative effects that the regular presence of humans may be having on the local soundscape. This result was not detected through more traditional assessments of diversity and may provide support for the use of soundscape ecology as a biodiversity monitoring tool. However, this effect requires confirmation through further research, and we need a better understanding as to how these soundscape patterns reflect underlying changes in community biodiversity. We also need to know how the acoustic diversity indices perform under different circumstances, particularly in tropical forests environments, before adopting soundscape studies as a primary method for tropical forest conservation assessment.

6.2 Introduction

Tropical forest environments are particularly challenging to sample through traditional biodiversity survey methods, as the vegetation is often dense,

organisms are found in complex vertical and horizontal spatial distributions and vary temporally in activity, both daily and seasonally (DeVries, Murray & Lande 1997). Any one survey technique will normally only be able to target a small subset of the taxa present, and the extreme biodiversity complicates the identification of even the best-known groups (Basset *et al*. 2004; Sutherland 2006). In rainforests, where visual signalling is limited by the dense vegetation, acoustic communication can be particularly important, resulting in exceptionally acoustically rich environments (Farina 2014). One of the most striking features upon entering a rainforest is the soundscape; the high diversity of insects, birds, frogs and other sound producers creates a rich combination of songs and calls that hint at the high biodiversity contained within the forest. A relatively recent approach to environmental assessment is through the quantification and comparison of the soundscape itself (Sueur *et al*. 2014b).

The soundscape is considered to be "the collection of biological, geophysical and anthropogenic sounds that emanate from a landscape and which vary over space and time, reflecting important ecosystem processes and human activities" (Pijanowski *et al*. 2011a). Three key components of the soundscape have been identified: biophony, which includes all vocalisations, stridulations and other sounds produced by living organisms; geophony, which covers all sounds with a geophysical origin, such as earth vibrations, wind, rain and river sounds; and finally anthropophony, which covers all sounds produced by human activity, such as engine noise, drilling, music and talking (Pijanowski *et al*. 2011a). Biophony typically occupies frequencies above 1.5-2 kHz, whereas anthropophony and geophony predominate in the 0-2 kHz bands (Pijanowski *et al*. 2011b; Pieretti & Farina 2013; Duarte *et al*. 2015).

The soundscape has been suggested to change predictably in response to changing ecological and disturbance gradients and reflect changes in species richness and composition (Pijanowski *et al*. 2011a). There are multiple theories as to why the biophonic soundscape changes in response to environmental disturbance, including the acoustic niche hypothesis (Krause 1987) and the acoustic adaptation hypothesis (Morton 1975). The acoustic niche hypothesis poses that organisms within an ecosystem co-evolved to optimise the frequencies and timings of their calls to avoid masking one another. Therefore, a complete assemblage will occupy a wide range of frequency bands and have high

temporal coverage, which will be disrupted if species are added or removed from the system (Morton 1975). Evidence of animals adjusting their calling behaviour based on the frequencies occupied by other species (including invasive species and anthropogenic noise) has been found in several studies (Stone 2000; Both & Grant 2012; Villanueva-Rivera 2014). The acoustic adaptation hypothesis suggests that species' communication methods are carefully adapted to maximise transmission within their given physical environment. Support for the acoustic adaptation hypothesis is mixed, with more evidence for environmental adaptation of calling behaviour found for anurans and mammals than for birds (Ey & Fischer 2009). Changes in this environment due to disturbance, such as changes in vegetation structure, temperature and humidity, may mean that these communication methods are no longer optimal, with consequences for breeding success, predator avoidance and other important biological processes that depend on communication (Krause 1987). Changes in the acoustic patterns of the soundscape can therefore be an effective way to assess the health of a biome and to detect changes that may indicate the ecosystem is being degraded (Krause 1999; Farina 2014).

Soundscape quantification has been suggested as a cost-effective method for monitoring tropical forest environments, as remote recording devices can be distributed throughout the area of interest to collect data for days, weeks or even months at a time, with limited human input required, which has the added benefit of removing the effect of human presence during recording (Farina 2014; Pieretti *et al*. 2015). This would make soundscape recording a potentially valuable complementary method to go alongside traditional biodiversity surveys, and may also provide additional value as acoustic time capsules for future reference (Sayuri, Sugai & Llusia 2019). The acoustic data collected can then be analysed to describe the characteristics of the soundscape by quantifying the contributions of different frequencies over time using acoustic diversity indices, without the need to manually listen to the recordings and identify the species present (Pijanowski *et al*. 2011b). There are many acoustic diversity indices available, and part of the current challenge is to identify which of these are most suitable for different applications (Sueur *et al*. 2014b; Fuller *et al*. 2015); however, this is to be expected considering the field of soundscape ecology has emerged relatively recently and makes research on this topic all the more

necessary. Acoustic ecology is a rapidly developing field, with the Journal of Ecoacoustics established in 2017. There has been a lot of excitement about the potential of this approach to help us detect changes in the environment (Deichmann *et al*. 2018), and it has many potential advantages, including 24 hour sampling without an observer effect, and the ability to capture a large proportion of the sound-producing community, not just specific target taxa. The increase in low cost devices such as the AudioMoth (Hill *et al*. 2018), improvements in analysis (Sueur 2018) and the promising correlations found in many studies (Depraetere *et al*. 2012; Gasc *et al*. 2013a; Bobryk *et al*. 2015) do suggest that soundscape ecology has the potential to make a valuable contribution to our biodiversity monitoring toolkit. However, I believe that much more work is required to establish best-practise sampling schemes and to identify suitable diversity metrics that perform consistently well in different environments before soundscape diversity should be used as a primary source of data on biodiversity responses.

In some case, acoustic diversity correlates well with species richness (Depraetere *et al*. 2012; Tucker *et al*. 2014; Bobryk *et al*. 2015), diversity and evenness (Harris, Shears & Radford 2016) and phylogenetic and functional diversity (Gasc *et al*. 2013b). However, studies on this topic are so far limited, and further research is required to test which acoustic indices best correlate with different components of biodiversity in a range of habitats and conditions. One recent study compared how well several acoustic indices correlated with bird diversity estimated from point count surveys in China, and found that none showed a strong correlation, but that acoustic entropy, evenness and acoustic diversity performed best (Mammides *et al*. 2017). A similar study in Brazil found the acoustic complexity and bioacoustic indices correlated with bird diversity detected through point counts (Jorge *et al*. 2018).

As an ecological monitoring tool, acoustic diversity has been successfully used to detect differences between disturbed and undisturbed habitats due to a variety of human impacts. Changes in the biological community and the geophysical environment in response to climate change (loss of species and reduced water flow) have been detected through changes to the geophony and biophony (Krause & Farina 2016). Pekin *et al*. (2012) found that acoustic diversity correlated well with forest canopy structure, and with the degree of

fragmentation and ecological condition, with high acoustic diversity in better preserved sites (Tucker *et al*. 2014; Fuller *et al*. 2015). In response to human disturbance, acoustic diversity and evenness tends to be highest in intact natural landscapes and decrease with increasing human disturbance (Slabbekoorn 2004; Sueur *et al*. 2008; Pijanowski *et al*. 2011b). One of the only studies examining soundscape diversity across a gradient of human modification in tropical forest was conducted in Papua New Guinea and found that when forest cover was fully retained, there was much higher soundscape saturation at peak acoustic activity times compared to areas with fragmented forest cover. Even mild human activity substantially diminished the sound-producing biodiversity and led to a loss of distinct dawn and dusk choruses (Burivalova *et al*. 2018). In some cases, the patterns of acoustic diversity in response to human disturbance are more complex. A weak trend of increased biophonic diversity with decreased disturbance intensity was found in response to proximity to a gas drilling platform in the Amazon, but anthropophonic diversity was higher close to the platform (Deichmann *et al*. 2017). Patterns may also vary temporally, with acoustic complexity found to increase with distance from mining activity in tropical forest at night, but be higher close to the mine during the day (Duarte *et al*. 2015).

I aimed to investigate whether acoustic diversity measures can be used to detect a response by the biological communities across a gradient of human disturbance in regenerating tropical forest in Peru. I chose to use the acoustic diversity, acoustic evenness and acoustic complexity indices, as these are some of the most established in the field and have been shown to correlate with disturbance and diversity in previous studies (Pijanowski *et al*. 2011b; Pieretti, Farina & Morri 2011; Duarte *et al*. 2015; Mammides *et al*. 2017; Jorge *et al*. 2018). My hypothesis was that increased human disturbance, in the form of forest conversion to agriculture, leads to an overall loss of species and change in community composition which will include a loss and disruption of sound-producing species. I predicted that this will be detected as loss in acoustic diversity, acoustic complexity and acoustic evenness with increased disturbance intensity across the study gradient.

6.3 Methods

6.3.1 Study area

Research was conducted in and around the Manu Learning Centre (UTM Zone 19L 240350 E, 8584900 S, 470 m above sea level) in the cultural zone of the Manu Biosphere Reserve in southeast Peru. As in previous chapters, the study covered a gradient of disturbance from minimally disturbed tropical forest to banana monocultures, sampling 18 sites across six levels of disturbance intensity. For full details of the sampling sites and study area, please see Chapters 2.

6.3.2 Data Collection

Acoustic recordings were carried out at each site using SM2+ Songmeter recorders by Wildlife Acoustics, each with one microphone. Three recorders were used so that three sites were sampled simultaneously to reduce the effect of temporal variation between recordings. The recorders were also rotated between sites to avoid any effect of differences between recorders. All recorders were set up for mono recording with a 16-bit sample rate of 96000 Hz, a 3 Hz low-pass filter and 48 dB gain and located at a height of 1.5m to ensure that vegetation did not interfere with the microphone (Pieretti *et al*. 2015). The daily recording programme consisted of a 1 minute recording every 15 minutes throughout the 24 hour cycle (Pieretti *et al*. 2015). Recordings were carried out between 8th September to 7th October 2015 and 19th September to 20th October 2016. The recorders were in the field for a total of 3066.5 hours (recorder 1: 764.45 hours, recorder 2: 999.38 hours, recorder 3: 1302.67 hours; four minutes of data were collected each hour).

Each site was sampled for a minimum of two days (48 hrs) each year and longer where possible. This had to be scheduled around days when staff were available to set up and collect the recorders and was limited by the number of recorders available to be rotated between all the sites in the time available for sampling. I used one recorder on one side of the river and two on the other at any time, and alternated which side had more recorders. The recorders were usually put out first thing on Monday morning, moved to a new location on Wednesday afternoon, and collected back in on Saturday in order to be compatible with the field team's work schedule. I excluded samples around the times the recorders

were moved to avoid including recordings of human voices. Periods of heavy rain resulted in some poor quality recordings, either dominated almost completely by the geophony or with clipping due to high volume; therefore, I used the weather data to exclude recordings from days with >30mm rainfall (Depraetere *et al*. 2012). There were also a few instances where the microphone was damaged by water and the recordings were corrupted, so I excluded those recordings where the acoustic diversity or evenness indices hit a maximum or minimum value and remained there continuously for multiple hours or days. After this cleaning of the dataset, I combined the data from 2015 and 2016 and kept the first suitable 190 one-minute samples for each site from each year to obtain approximately equal sample sizes for each site (n = 380 minutes per site, or as close as possible). I aimed to sample evenly from each year but, in some cases, samples lost due to damaged recordings meant this was not possible, so additional samples were used from the other year, if available. A total sample size of 6600 one-minute long clips were used for the analysis, which was about 50% of the total data collected, emphasising the importance of allowing sufficient recording time to account for weather and potential negative impacts on the data quality.

Analysis of the data was carried out in R version 3.4.1 (R Core Team 2017). Acoustic diversity, complexity and evenness were calculated using the package soundecology (Villanueva-Rivera & Pijanowski 2016). For all indices, a maximum frequency threshold of 22,050 Hz was used and for the calculation of acoustic complexity a minimum frequency filter of 1500 Hz was applied. This low frequency filter reduces the influence of geophony and anthropophony on the complexity index and concentrates instead on the signal from the biophony (Sueur *et al*. 2008; Krause, Gage & Joo 2011; Pieretti & Farina 2013; Duarte *et al*. 2015).

The acoustic evenness index calculated in the soundecology package is based on the Gini coefficient of evenness (Gini 1912; Villanueva-Rivera *et al*. 2011), in which a high value represents a less even community. The acoustic evenness index works by dividing the recording into frequency bins (default size of frequency bands 1000 Hz) and then assessing the proportion of signal over a 50db threshold in each bin (Villanueva-Rivera *et al*. 2011). This is then used to calculate the dominance of each frequency band, from which the Gini coefficient is obtained, describing how evenly represented these frequencies are

in the recording. The raw Gini outputs were used in the statistical analyses (and all tables in the supplementary materials). However, to present the results in the most intuitive way, throughout the main text 'acoustic evenness' refers to the inverse of the Gini coefficient: this means high evenness index values can be directly interpreted as high evenness of the acoustic community. For the acoustic diversity values, which is a form of Shannon diversity based on frequency bands, again, the original output of the formula was used for the analysis and in the supplementary tables. The diversity is calculated by dividing the frequencies into bins (default size of frequency bands 1000 Hz) and then calculating the proportion of time that band is occupied with sound (a measure of the abundance of the frequency). Then the Shannon index is applied to the fraction of sound in each frequency (Villanueva-Rivera *et al*. 2011). For ease of interpretation, the exponential acoustic diversity values are presented throughout the main text and results. The exponential Shannon diversity results reflect the effective number of acoustic frequencies present (alpha diversity at q = 1), just as the effective number of species were used in previous chapters. For additional context in relation to previous chapters of this thesis, the Gini coefficient is directly related to the Simpson index (alpha diversity at q = 2) but here remains scaled between 0 and 1. Acoustic complexity (ACI) is calculated by again dividing the frequencies into bins but then a different approach is used, where the difference in the intensity of sound is compared between two adjacent timesteps (default size 5s), in each frequency bin. This is done for each timestep in each frequency bin, and then the total acoustic complexity of the recording is the sum of these (Pieretti, Farina & Morri 2011). This means that the ACI is particularly sensitive to sounds that change intensity frequently (on/off sounds), whereas both acoustic diversity and acoustic evenness will be maximised by having many frequency bands occupied for large proportions of the time. Spectrograms were plotted in R using the packages seewave (Sueur *et al*. 2014a) and tuneR (Ligges *et al*. 2017), and filters in Audacity 2.1.3 were used to identify some of the sources of sounds at different frequencies in the recordings.

After calculating the diversity indices for each sample, I used Spearman rank correlation tests (Spearman 1904) to see if there was any correlation between acoustic diversity, complexity or evenness with disturbance rank (Table S6.1). I first looked at the pattern of soundscape diversity in response to disturbance for

the overall recording period, and then examined how the acoustic diversity indices changed within a site over the course of the day, to see if there was any pattern that might suggest a key time for soundscape comparison. To see if the strength or direction of the relationship changed throughout the day, I concentrated on snapshots of time, calculating the correlation between the acoustic indices and disturbance at three-hour intervals. Each time snapshot included the samples collected within 30 minutes either side of the defined time (four minutes in total). As well as calculating the correlation with disturbance at each timepoint, I used a permutation test to calculate the combined p value for the correlation between disturbance rank and soundscape diversity across all timepoints (00:00, 03:00, 06:00, 09:00, 12:00, 15:00, 18:00 and 21:00) to see if there was a consistent effect of disturbance once temporal variation was removed.

In addition to the correlation tests, where a significant correlation was detected I also used general linear mixed models to check the patterns identified while controlling for the effects of elevation and distance to river, with a random effect for the Songmeter recorder used (packages *lme4*, Bates *et al*. 2015 and *car*, Fox & Weisberg 2011; Table S6.2 and S6.3). The residuals of these models were tested for spatial autocorrelation using Moran's I (package *ape*, Paradis *et al*. 2004). The spatial autocorrelation check indicated potential spatial autocorrelation in the models in a few cases, but the effect size was small (<0.03) and the pattern was not consistently present, so this was not considered a cause for concern (Table S6.4). Finally, in order to explore the possibility that the noise from the research station and researchers in the field might have affected the soundscape patterns observed, I compared the acoustic diversity in disturbance ranks 4-6 using linear models of each acoustic index with rank and distance from the MLC research station (the closest proxy of field staff traffic available) as the explanatory variables.

6.4 Results

There was a significant weak correlation between disturbance rank and acoustic complexity (rho = -0.16, p < 0.001), acoustic diversity (rho = -0.17 , p < 0.001), and acoustic evenness (rho = -0.15, p < 0.001). Overall, acoustic complexity, acoustic diversity and acoustic evenness all increased with increasing disturbance intensity (Figure 6.1). However, closer examination of the patterns of soundscape diversity seen across the gradient, particularly acoustic diversity and evenness shows that the trends appear to be strongly influenced by the data from ranks 4-5 (Figure 6.1), and mainly during working hours (07:00-00:00; Figure 6.3).

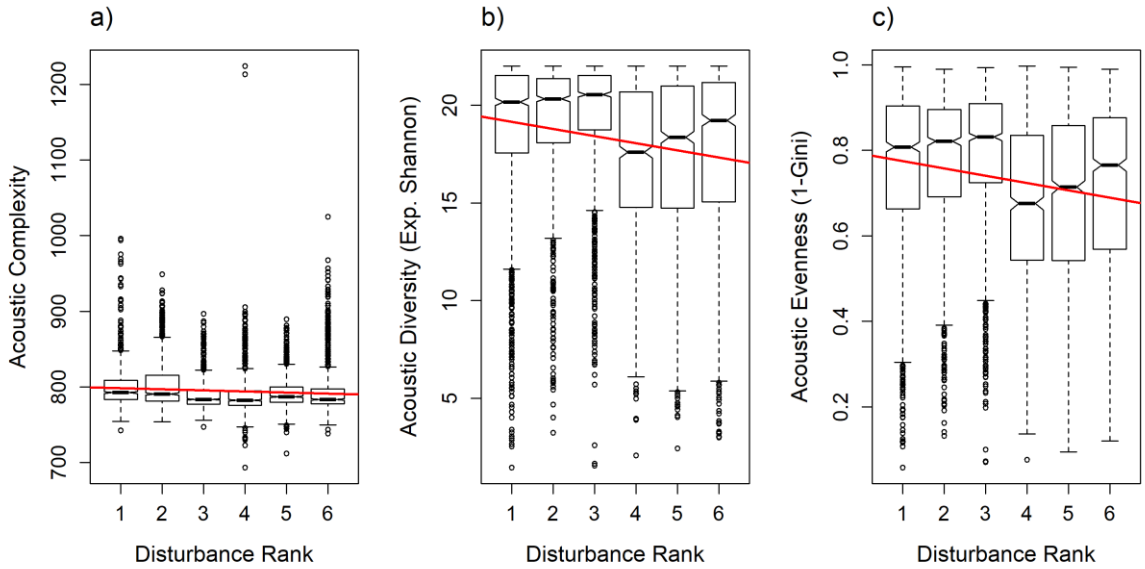

Figure 6.1 Changes in (a) acoustic complexity, (b) acoustic diversity (exponential Shannon index) and (c) acoustic evenness (inverse Gini coefficient) across the disturbance gradient. Disturbance rank runs from 1 (most disturbed) to 6 (least disturbed). Boxplots show median and first quartile of data, with whiskers extending to third quartile, and non-overlap of box notches indicating if medians differ (Chambers *et al.* 1983). Each data point is the soundscape diversity value for a minute of recording at a site, and the red line indicates the linear regression trend between each acoustic index and disturbance rank.

When the data from the agricultural zone (ranks 1-3) and the reserve (ranks 4-6) are considered separately, each of these show the expected trend predicted by my initial hypothesis of increased acoustic diversity, complexity and evenness as disturbance intensity decreased (Figure 6.1). Yet when comparing across the full gradient, ranks four and five have much lower acoustic diversity than the agricultural sites, which results in the opposite trend emerging overall. After analysing ranks 4-6 independently and including distance to the research station in the model, I found distance to the research station explained significant

additional variation compared to disturbance rank alone for acoustic complexity (est. coeff. = -0.00004, p = <0.0001) and acoustic evenness (est. coeff. = 0.0004, p = <0.0001) but with very small effect sizes. No additional significant variation in acoustic complexity was explained by including distance to the MLC (est. coeff. = <0.0001, p = 0.09) compared to the model with disturbance rank alone.

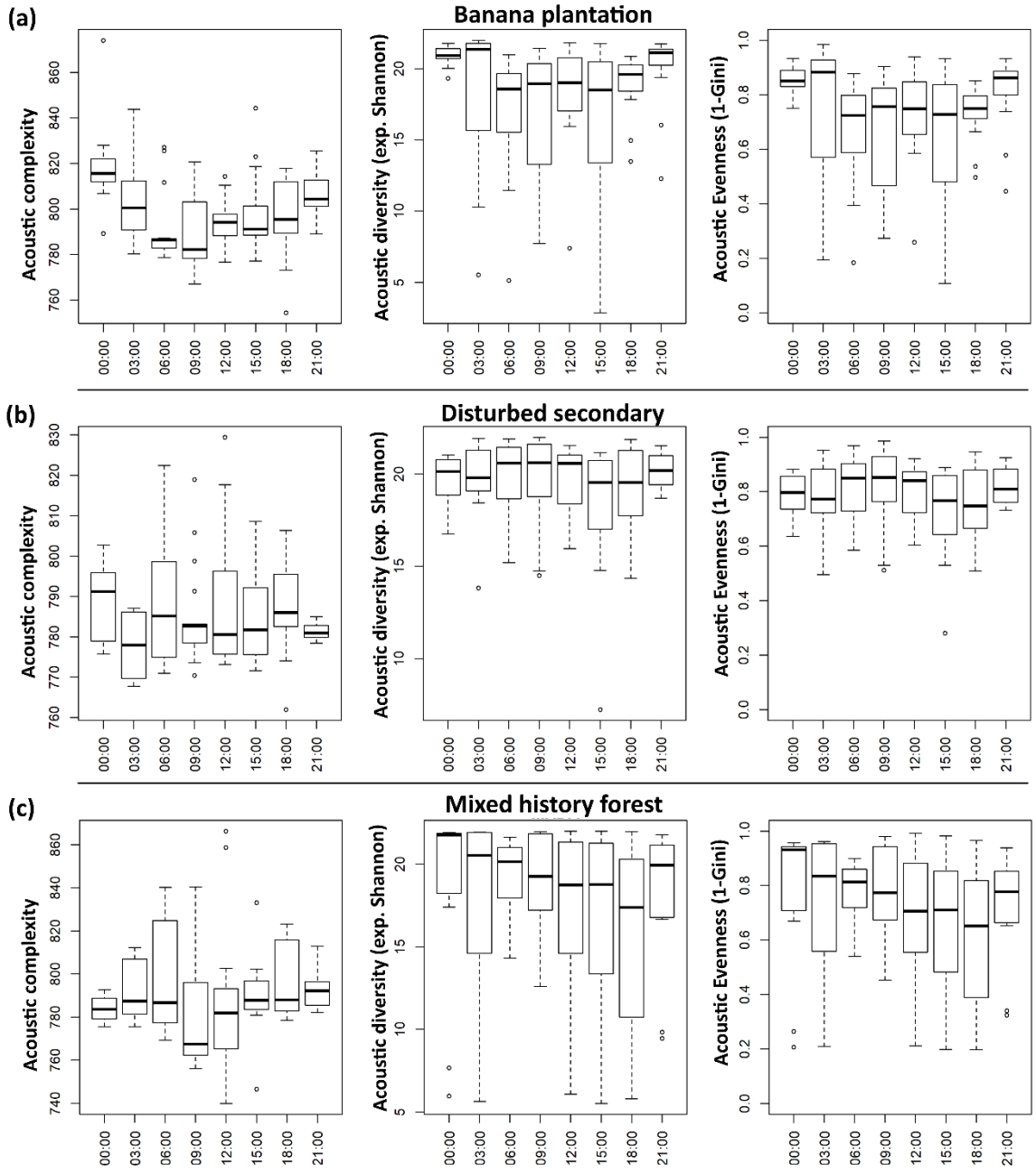

Figure 6.2 Variation in the soundscape diversity indices within a site over time: acoustic complexity, acoustic diversity (exponential Shannon) and acoustic evenness (inverse of the Gini coefficient). Comparison of three sites: (a) banana, (b) secondary and (c) mixed history forest, all sampled in the same weeks. Boxplots show median and first quartile of data, with whiskers extending to third quartile, and circles for data points beyond this.

On examining the within-site temporal variation in soundscape diversity, I found that there was a high amount of variability (Figure 6.2). However, there was no consistent pattern of peaks in any of the indices at particular times of day that could be detected across sites. Because of the high level of temporal variation in soundscape diversity within sites, I tested the correlations between each soundscape diversity index and disturbance rank at specific times throughout the day. This allowed me to focus on the correlation between disturbance and soundscape diversity in the absence of the temporal variation. There was a consistent negative correlation between disturbance rank and soundscape diversity (Figure 6.3), although the strength of the correlation varied depending on the time of day. When the overall pattern of the individual correlations at the different times of day were considered together, there was a highly significant correlation between soundscape diversity and disturbance rank (permuted combined p-value <0.0001). Acoustic complexity was significantly negatively correlated with disturbance rank at 00:00, 09:00, 12:00, 15:00 and 21:00, as was acoustic diversity at all time tested except 00:00 and 06:00. Acoustic evenness also showed a significant negative correlation with disturbance rank from 09:00 to 21:00, but not from 00:00 to 06:00. The strengths of the correlations were generally weak (rho > -0.20) but did exceed rho < -0.20 at several times for each of the indices. However, the strongest correlations for each index did not all occur at the same times of day.

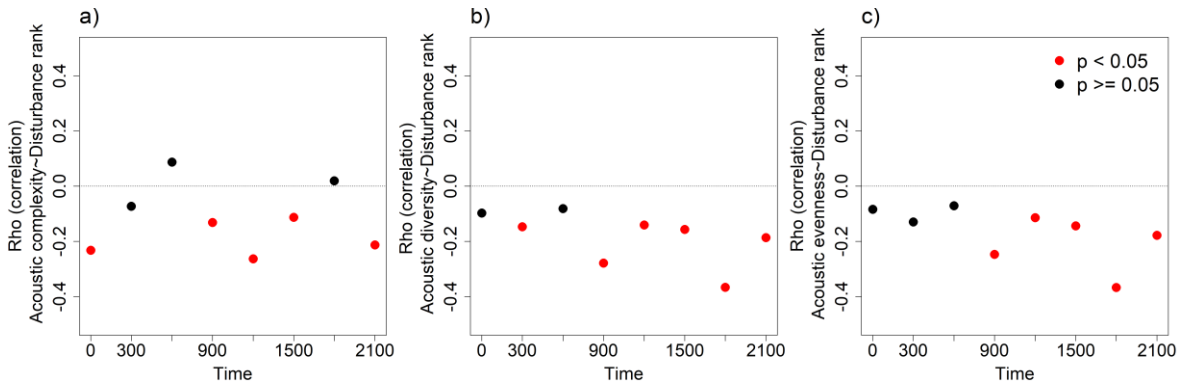

Figure 6.3 The strength of the Spearman rank correlations between acoustic complexity, diversity and evenness (inverse of Gini coefficient) with disturbance rank at each time of day. Where the correlation was statistically significant, the circles are filled red, and remain black if the correlation was non-significant.

A more detailed overview of one of the time snapshots captured in Figure 6.3 is provided below, showing the relationship between soundscape diversity and

disturbance at 12:00 (Figure 6.4). There was a significant positive correlation between disturbance rank and all three indices: acoustic complexity (rho = -0.26, p < 0.001), acoustic diversity (rho = -0.14, p = 0.010) and acoustic evenness (rho = -0.11, p = 0.036). However, for comparison, during the dawn chorus at 06:00 there was no significant correlation between disturbance and any of the acoustic indices (Figure 6.5), and acoustic complexity even showed the opposite trend (Figure 6.5a) although this was not significant.

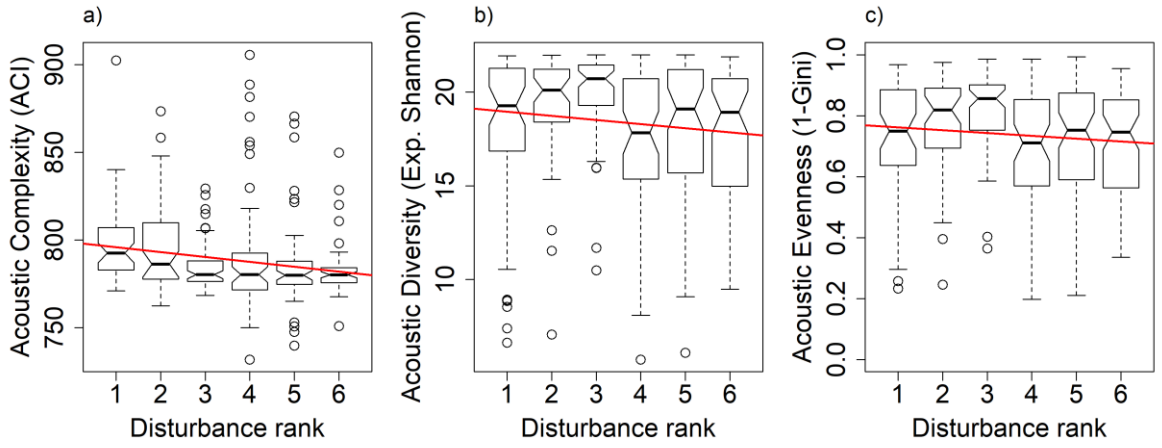

Figure 6.4 Changes in acoustic diversity, complexity and evenness (inverse of Gini coefficient) across the gradient at 12:00. Acoustic complexity, diversity and evenness all have a significant negative correlation with disturbance rank (rank 1 = most disturbed).

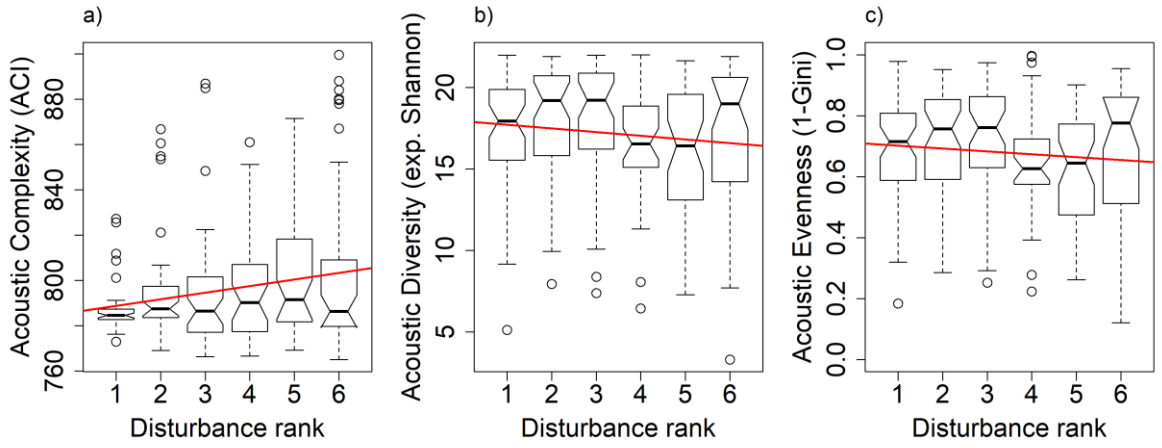

Figure 6.5 Changes in (a) acoustic complexity (b) acoustic diversity (Shannon) and (c) acoustic evenness (inverse of Gini coefficient) across the gradient at 06:00. There are no significant correlations between acoustic complexity, diversity or evenness with disturbance rank (rank 1 = most disturbed), and acoustic complexity shows a positive trend with disturbance rank.

On inspection of a selection of spectrograms of our samples, I found that insects were the most dominant component of the soundscape, particularly cicadas and Orthoptera, with birds and frogs also regularly detected in the recordings (Figure 6.6). There was no obvious change in the dominant groups of the soundscape

across the gradient that I was able to detect by visual or audio comparison of the spectograms.

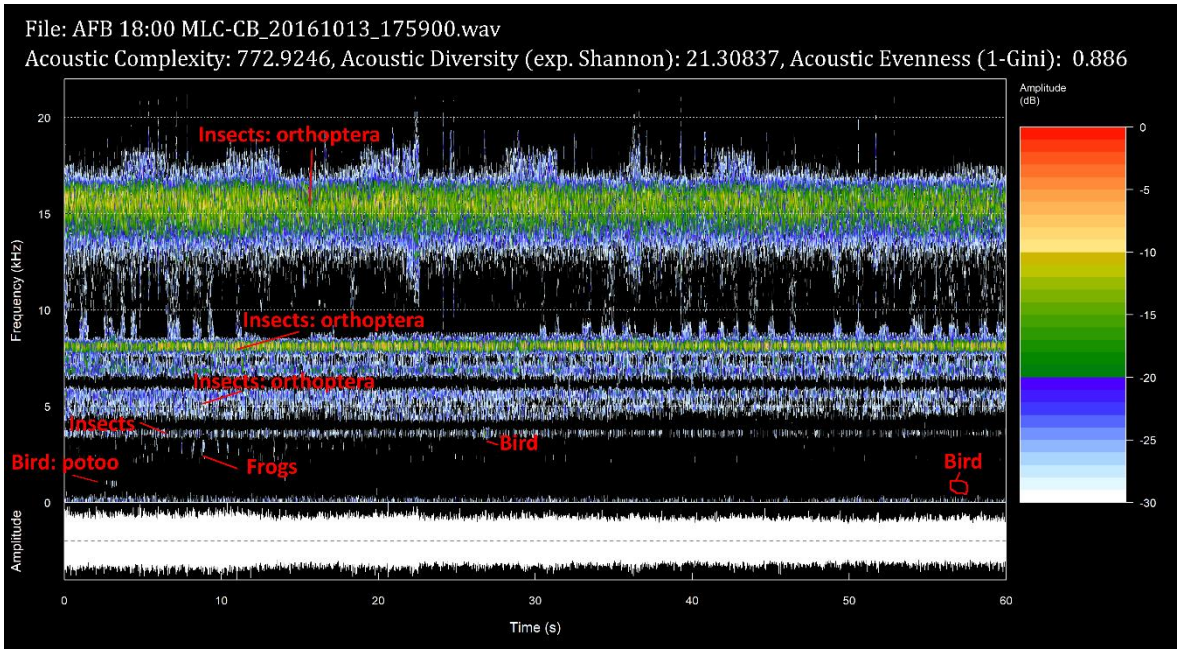

Figure 6.6 Spectrogram of a sample taken at 18:00 at site AF-B (disturbance rank 2), showing the peak frequencies present and labels indicating the identity of the sound producers. Plotted with the package seewave (Sueur *et al.* 2014a) in R, using the default FFT size.

6.5 Discussion

My results indicated an increase in acoustic complexity, acoustic diversity and acoustic evenness as disturbance intensity increased. This was contrary to expectations: I predicted that complexity, diversity and evenness would be highest in the undisturbed forest and low in the highly disturbed sites, based on the acoustic niche hypothesis that the more species present the greater variety of acoustic niches (e.g. frequency bands/call phenology) they would occupy, as well as the findings of previous studies. These results contrast strongly with the findings of the previous chapters of this thesis, in which I found a clear negative impact of human disturbance on biodiversity. It is difficult to know whether these results reflect true differences in the soundscape in response to disturbance; although the results show an increase in soundscape diversity with increased disturbance, this pattern is not consistent across the disturbance ranks and it is possible that there is no difference in the soundscape across the gradient. It is also possible that the acoustic diversity measures used in this study were not able to detect differences in the soundscape in this complex tropical rainforest environment. A priority for soundscape ecology research should be to improve our knowledge of what the acoustic diversity measures

reflect in terms of the biological communities and which indices are the most suitable for different environments.

Following the methodology of previous studies, a 1.5 kHz filter was applied to the data for calculating the acoustic complexity index. The aim of this was to filter out the geophony and anthropophony and focus instead on the core of the biophony (Pieretti & Farina 2013; Duarte *et al*. 2015). However, on examination of the spectrograms, I found that a few of the animal calls detected, particularly birds, fell below this frequency threshold (e.g. the potoo *Nyctibius* spp. in Figure 6.6), so the use of this filter may have underestimated the acoustic complexity of the sites, and may have been important for nocturnal species in particular. On visual and audio inspection of the data, there was no indication that these were biased towards any end of the disturbance gradient. Whilst a filter is desirable to prevent non-biological noise obscuring biological acoustic patterns, further research is required to determine the most appropriate filter threshold for use in tropical forests. No filter was used for the acoustic diversity or acoustic evenness indices.

The patterns of soundscape diversity found in this study were contrary to my prediction that increased forest disturbance would lead to a decrease in acoustic complexity, diversity and evenness. Part of the reason I did not see a drop in acoustic diversity and complexity with increased disturbance may be because the most dominant components of the soundscape were insects, particularly cicadas and Orthoptera such as crickets (Aide *et al*. 2017). It is possible that these groups persist quite well in the types of disturbed habitat included in this study and obscure the loss of specialised forest species that call less often and cover fewer frequency bands, although Orthoptera have been suggested as sensitive indicators of habitat quality (Riede 1998). In the case of acoustic diversity, the issue of shifting baselines may be particularly important, and we have no way of knowing how even the least disturbed site compares to its historical assemblage. If species have been added or lost, disrupting the acoustic niche space (Krause 1987), the acoustic signal might show evidence of disturbance even if species diversity remains high. Another factor that may have contributed to the higher-than-expected acoustic diversity of the most disturbed sites is that sound carries further in open habitats than in denser vegetation (Farina 2014). This may mean that the recordings from the more open banana

and agroforestry plantations include calls from slightly further away than the recordings collected in the more sound-dampening undisturbed sites. I did not manage to find any way of controlling for this possibility, but in future studies it could be worth testing the differences in detectability between habitat types to assess how important this might be. If there was no notable difference in the abundance and diversity of sound producing animals found across the gradient, this potential detectability issue may have tipped things in favour of the more disturbed sites and could partially explain the unexpected pattern observed. The Songmeter guidance advises that detectability will vary depending on the volume and direction of the source, as well as humidity and vegetation, but that, as a guide, if you can hear it by ear it will be detected by the recorder (Wildlife Acoustics 2018). The temporal variation in the acoustic diversity at a site, as seen in Figure 6.2, adds additional complexity to trying to establish a suitable sampling strategy and to interpret the results, as there is no clear time of day when the different habitats appear to show a clear peak when we might target recording. There is a similar amount of variation with a site across the day as there is between sites, and they do not follow the same patterns. This may be due to different combinations of species calling at different times, and the distribution and behaviour of these may differ across the gradient, particularly if calling behaviour is triggered by factors such as light or temperature, as it may get darker earlier under the forest canopy, for example, than in the open plantations. Animal calling behaviour is highly complex and adds further difficulties to the challenge of interpreting soundscape diversity patterns across different habitat types.

One other possible explanation for the unexpected trend of higher acoustic diversity with increased disturbance is the influence of a considerable human presence (research staff and volunteers) in parts of the study area. Disturbance ranks 4-5 contained the sites closest to the research station (Figure 2.5), through which the field team pass daily to access their research sites. Usually, there would be three to five groups, each consisting of around three or four people (researchers and volunteers) daily, plus one or two small tourist groups each week. The Crees Foundation did have protocols advising people to keep conversation and noise in general to a minimum when in the forest, but this was not always followed. Conversely, the heavily disturbed sites (ranks 1-3) are

visited by people much more rarely, with most farmers visiting to their plots less than once a fortnight. Therefore, I suspect that the unexpected results of this study (higher acoustic diversity and lower evenness in more disturbed sites) may be partially driven by the noise created by staff and volunteers working within the reserve, talking and walking noisily and potentially impacting the presence and calling behaviour of species in the area (Iglesias, Diaz-Balteiro & Soli 2014). Changes in calling behaviour by species can be a short-term response to an immediate perceived threat, but if it happens frequently this can be detected as a long-term effect. Noise from the research station itself, such as music, construction and generator noise, may also affect the presence or calling behaviour of species in the nearby area (Potvin 2017). The results of the linear models of acoustic diversity in ranks 4-6 that included distance to the research station indicated that this may be the case, though the effect size was small. Unfortunately, our study was not designed to assess the impact of field researchers as a source of disturbance, so the strength of the conclusions that can be drawn from this is limited.

Due to shifting baselines, we cannot know how closely the least disturbed forest reflects its pre-disturbance state, as even those sites have people passing through regularly, though less frequently and in smaller numbers than sites nearer camp. Another difficulty with shifting baselines is how to define 'pre-disturbance', as humans have been influencing this landscape for centuries, including the rubber trade in the 1800s and petroglyphs dating back to around 1000 AD (MacKay 2015), although the impact of small populations with limited technology would have been significantly lower than the current disturbance intensity. Previous research comparing forests of different disturbance levels at the MLC found diversity to be highest in the least disturbed (rank 6) forest compared to the cleared regenerating (rank 4) forest (Whitworth 2016) but that the reserve as a whole held comparable levels of biodiversity as nearby areas of primary forest (Whitworth *et al*. 2016b).

During the dawn chorus at 6am, I detected a decline in acoustic complexity with increased disturbance (Figure 6.5); it may be that at this time of peak biophony and minimal anthropophony, the signal is strong enough to detect the effect of forest vegetation disturbance (Burivalova *et al*. 2018), but at other times of the day, this is masked by the ongoing human disturbance from the research team.

The effect of researcher presence on the soundscape has been acknowledged as an issue in other research published earlier this year (Jorge *et al*. 2018). The potential impact that researchers and volunteers may be having on the soundscape of the reserve they are aiming to protect is of concern and warrants further research.

Not only is the soundscape a potentially useful indicator of the responses of the biological community to human disturbance, but the soundscape itself possesses ecological and social value and should be considered a resource to be carefully managed and protected (Dumyahn & Pijanowski 2011). Many animals rely on an intact soundscape in order to detect predators and prey, and to find partners for breeding, and they experience stress in response to noise pollution (Francis & Barber 2013; Shannon *et al*. 2016). Humans visit national parks and other natural landscapes, including rainforests, to experience the natural environment, which delivers many wellbeing benefits, but polluted soundscapes negatively impact on this experience and can have negative consequences for health, stress and quality of life (Dumyahn & Pijanowski 2011; Iglesias, Diaz-Balteiro & Soli 2014).

There are many acoustic indices in use, with little consistency between publications as to which indices they use. Different habitat types present very different soundscapes for analysis (Krause, Gage & Joo 2011), and the characteristics of these may influence which measures work best. For example, lower correlations between avian biodiversity and acoustic diversity have been found in neotropical forests compared to temperate forests (Eldridge *et al*. 2018). Soundscape ecology still lacks sufficient evidence for the best approaches for quantifying soundscapes and identifying how well different indices perform under different conditions, although this is an active area of research (Buxton *et al*. 2018). This makes it impossible to compare the acoustic diversity of the sites in this study against those found in other studies, as in all cases the recording methodologies or the choice of index are slightly different (Gasc *et al*. 2013a; Towsey *et al*. 2014; Tucker *et al*. 2014; Burivalova, Şekercioğlu & Koh 2014; Pieretti *et al*. 2015). The nearest comparable study I found was from the Atlantic forest in Brazil, where acoustic complexity ranged between approximately 100-400 (Pieretti *et al*. 2015) — much lower than the ACI values of 700-900 found at my sites, suggesting my sites may have very high acoustic complexity throughout the disturbance gradient. However, it is likely that a

considerable proportion of the differences in the absolute values could be due to differences in the recording or processing methodologies, highlighting the need for more research to determine appropriate standardised methods to enable easier comparisons. The wide choice of acoustic indicators is also an issue in the same way as for traditional biodiversity indices; the choice of acoustic index can make the difference as to whether or not a response to disturbance or a correlation with species richness is detected (Sueur *et al*. 2014b; Fuller *et al*. 2015; Lamond 2016). The indices used in this study were chosen because they are some of the most established in the field and have been found to perform well in several previous studies (Pijanowski *et al*. 2011b; Pekin *et al*. 2012; Pieretti & Farina 2013; Fuller *et al*. 2015). However, these indices also have their weaknesses: the acoustic complexity index correlates well with the number of bird vocalisations, but very flat, constant sounds such as insect buzzing can result in low ACI values (Pieretti, Farina & Morri 2011; Gasc *et al*. 2013a). Minimising the effect of these constant sounds can be useful for ensuring background geophony and anthropophony do not inflate the ACI, but also means that the ACI does not always increase as species are added to the soundscape, and in some cases may decrease, depending on the species added (Gasc *et al*. 2015). Several authors have compared multiple indices to assess their performance under difference circumstances, and the most predominant conclusion is that any soundscape study should use multiple acoustic indices, or even combinations of indices (Buxton *et al*. 2018; Eldridge *et al*. 2018), in order to maximise sensitivity and reliability (Gasc *et al*. 2013a, 2015; Sueur *et al*. 2014b; Towsey *et al*. 2014). This is a familiar message, as the need for using multiple diversity measures for traditional biodiversity assessments has been recognised (Chao *et al*. 2014; Reeve *et al*. 2016), and is heavily discussed in previous chapters of this thesis.

6.6 Conclusion

This is the first study that has used multiple acoustic diversity indices to identify how the soundscape changes across a gradient of human disturbance in neotropical forest, and my results were contrary to expectations. There was an overall increase in acoustic complexity, acoustic diversity and acoustic evenness detected in response to increasing disturbance intensity across the gradient. There was a large amount of within-site temporal variation in soundscape

diversity, but there was no time of day at which all three indices concurrently appeared most sensitive. When samples were compared at specific timepoints in the day, significant positive correlations between the soundscape diversity and disturbance rank were detected for the majority of timepoints tested, suggesting soundscape diversity is responding to disturbance even if these responses are non-intuitive.

The explanation for the unexpected pattern of increasing acoustic diversity with increased disturbance found in this study are difficult to ascertain from the data, but one explanation is that acoustic disturbance caused by humans within the reserve is negatively impacting the acoustic community. This possibility warrants further research into the impact of humans on soundscapes, as well as into how anthropogenic sounds influence the diversity indices. I also would like to highlight the need for more studies comparing the performance of different acoustic diversity indices, such as that Mammides *et al*. (2017), in order to ground-truth our understanding as to how different acoustic indices respond to communities of known diversity as well as when a particular index is most suitable and which combinations of indices are likely to be most effective. It would be valuable for such future research to compare acoustic indices using both artificially created recordings and field recordings accompanied by intensive traditional inventory data, and to cover a range of habitats, regions and target taxa. I hope this will lead to the development of more consistent methods of acoustic diversity quantification so that studies can be compared and interpreted more easily. Although often proposed as a quick and easy method, the costs and time involved in soundscape assessments are not trivial, and although costs are reducing with improvements in technology, data processing time is still high. I would strongly recommend against using soundscape recording as a primary assessment method for forest disturbance and conservation monitoring, but it has the potential to be a useful complementary method and also has significant merit as a way of capturing soundscape data for future reference (Sayuri, Sugai & Llusia 2019). If more consistent methods and interpretations can be established this would vastly increase the potential utility of soundscape indices for conservation and biodiversity monitoring in the tropics.

7 General discussion

7.1 Overview

In this thesis, I set out to explore how different potential indicator groups responded across a gradient of human disturbance in tropical forest, and to identify the most sensitive measures to use for detecting their responses. I was interested in the effects that human disturbance has on biodiversity and ecosystem functioning, and whether these effects could be captured using a one-size-fits-all approach to diversity measurement that would work well across taxonomic groups. To do this, I sampled across a gradient of human disturbance in Manu, Peru. The gradient covered a range of land uses, from banana plantations and agroforestry to various stages of regenerating and intact forest. I approached the problem of biodiversity measurement armed with a recently developed set of unified diversity measures (Reeve *et al*. 2016), which place alpha, beta and gamma diversity into a consistent framework (Chao, Chiu & Hsieh 2012) with a range of emphasis on rare species in the community. These measures are based on Hill numbers (Hill 1973) and directly related to traditional diversity indices, but include several novel aspects, including some new beta diversity measures and the power to incorporate species-similarity into the diversity calculation, adding an additional level of insight that has mostly been overlooked in biodiversity assessments before now. I also explored beta diversity through changes in community composition across the gradient using some alternative approaches based on ordination and dissimilarity (Legendre & De Cáceres 2013; Legendre & Gauthier 2014), to gain a further understanding of the impacts of disturbance on biodiversity.

I focused mostly on species-level diversity, specifically of a few insect taxa, but I also used a soundscape approach, which takes a step back from the individual level sampling and instead looks at the sound-producing community as a whole. Overall, biodiversity was found to respond negatively to human disturbance, but the most sensitive measures for detecting these changes varied between groups. Generally, alpha diversity changes were more easily detected using lower values of q, as rare species tended to be more sensitive to disturbance. Beta diversity assessment showed changes in community composition along the gradient and, in some cases, this was a larger effect than the change in alpha diversity. Species

richness was a sensitive measure of dung beetle disturbance responses, and to some extent also worked well for butterflies, but orchid bees responded much more strongly in abundance and redundancy. However, all three invertebrate groups showed a negative response to disturbance, yet the soundscape showed the opposing trend, with higher soundscape diversity in more disturbed forest.

7.2 Exploring the patterns

A loss of rare species and a decline in alpha diversity, particularly species richness, with increased disturbance supports the findings of other studies (Shackleton *et al*. 1994; Eggleton *et al*. 2002; Scheffler 2005; Alroy 2017). However, these measures were not always adequate for capturing the responses of the community, which could lead to the mistaken conclusion that the community is relatively insensitive to forest disturbance (also discussed by DeVries *et al*. 1997); and several studies, including those presented here, have found important changes in beta diversity in response to disturbance (Willott *et al*. 2000; Styring *et al*. 2011; Stork *et al*. 2017). Care should be taken in assessing whether biodiversity is impacted by disturbance, as important patterns could be easily overlooked by concentrating solely on one type of diversity. The reasons for the loss and change in species across the gradient could be due to a range of factors, including: changes in microclimate, such as temperature and humidity; a change in the plant communities, including the loss of important resource species, especially for the bees and butterflies. For dung beetles, the responses could be driven by a depletion of resources due to a loss of large mammals, which face greater hunting threats in the agricultural parts of the study area, or an adaptational mismatch for surviving in the changed environment, such as eyesight adapted to finding resources in dark, cluttered forest that does not work so well in bright, open habitats (Taylor *et al*. 2016). As seen in the dung beetle study, the changes in composition can have important consequences if functional groups are affected, such as the loss of larger beetles that are more effective at dung removal. I have illustrated this issue in just one of the taxa studied, but it is easy to imagine the implications of this when considered for the other wildlife present in this region; there are a vast number of species filling roles in a complex set of ecosystem functions, including large frugivores, carnivores, parasites and soil microbes. To further complicate matters, each of these exists as part of a network, with interactions and

feedbacks within and between species, so disrupting one component could have consequences throughout the system.

Generally, all three of the insect groups I studied showed a negative response to disturbance, but not all species followed this pattern. All three groups showed a decline in the observed species richness across the gradient, but the correlation between species richness and disturbance was strongest for the dung beetles (rho = 0.73). Alpha diversity at higher values of q were less strongly correlated with disturbance, which is unsurprising as tropical forests are well known for their high numbers of rare species (Hubbell 2013). However, it is important to consider multiple values of q, as in some cases, such as in prioritising conservation, rare species may be especially important, whereas in others, more common species may be of interest, such as in ecosystem function roles or the simple characterisation of a community. Furthermore, although tropical forests are known to have many rare species, the shape of the diversity profiles may be different in temperate regions and other habitat types, and it is worth capturing this variation to understand how communities with different evenness structures respond to changing environments. Abundance was found to be an insensitive measure for dung beetles (rho = -0.02) but showed a stronger correlation with disturbance for butterflies (rho = 0.8) and orchid bees (rho 0.63) than species richness. Beta diversity was important for all groups, with clear changes in species composition found in all cases, with high species turnover for dung beetles and orchid bees, and increased redundancy of the community found to correlate with increased disturbance for orchid bees and butterflies. Similarity-sensitive diversity was only considered for butterflies, but for this group similarity sensitive redundancy (rho = -0.76) and gamma diversity contributions (-0.81) were the measures that correlated most with disturbance, indicating that these are worth exploring further for other taxa. The decrease in species richness in areas of higher historical disturbance matches the patterns found for nocturnal birds, amphibians and butterflies across the same area (ranks 4-6) in a previous study (Whitworth 2016).

The response seen in acoustic diversity was somewhat surprising, since the overall pattern showed the opposite response to those seen in insect diversity. This suggests that care should be taken when using acoustics as an assessment tool for disturbance, as the results may not be completely intuitive. I explored

some of the possible reasons in Chapter 5, section 5.5, including the detection of human sounds within the reserve, and species producing sounds with very distinct characteristics that may differ in their contribution to acoustic diversity. However, for the moment I think the strongest conclusion from this work is that more research is needed to understand how the acoustic indices perform in tropical forest and what types and combinations of sound will result in high acoustic diversity scores. In addition to the research presented in chapter 5, I did a small test to improve our understanding of the acoustic diversity indices, where I combined multiple recordings into one sound file (same duration, with the sounds overlaying one another) and analysed the diversity of the original recordings and the combined ones. I did this for four different combinations of files, using either two or three files in each combination. I expected that since the combined recordings occupied more frequency bands and filled more of the recording time, the diversity indices would generally produce higher values for the combined recordings, with the possible exception of acoustic complexity. This was not the case; the patterns observed were roughly intermediate between the individual recordings, although not consistently (Figure 7.1). Although this test was only a crude example, it highlights that acoustic indices do not always work as you might expect. This is something people should be aware of when applying soundscape approaches to ecological assessments or conservation monitoring and emphasises the need for further research into how different acoustic indices work, and how they respond under different conditions and types of sound.

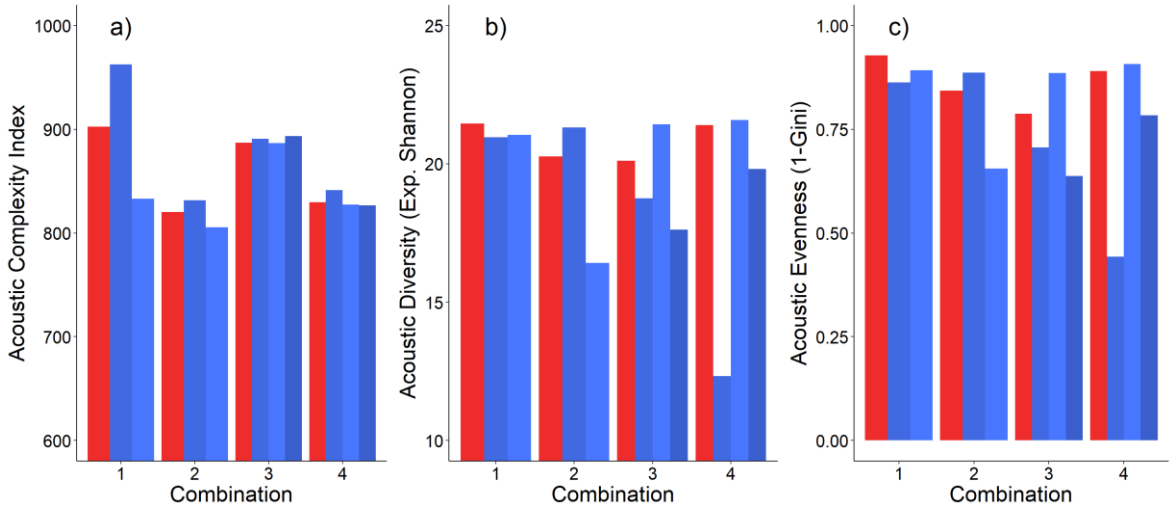

Figure 7.1 Comparing the (a) acoustic complexity, (b) acoustic diversity and (c) acoustic evenness of individual recordings (blue) compared to the diversity when those recordings are combined (red). Tested for four different combinations of recordings, with the files overlaid in Audacity.

I carried out several tests to try and determine if there was any evidence that ecosystem functions were being impacted by human disturbance. The results of these studies were mixed. I found evidence of a decline in secondary seed dispersal by dung beetles as disturbance increased, which could affect seedling survival and slow forest regeneration. This was similar to the results of Braga *et al.* (2013) but I did not find evidence for a reduction in nutrient cycling (dung burial) or soil aeration (excavation) by dung beetles. It would be expected that if the dung beetles are removing and burying the seeds, they would also be removing dung and burying it, thereby increasing soil aeration and soil nutrient levels. However, in my experiment soil and dung were not collected and weighed accurately, which is possibly why I did not detect any pattern. I found no change in the activity of generalist pollinators across the gradient, with the artificial flowers receiving similar numbers of visits from insect pollinators across the gradient, suggesting little cause for concern regarding general pollination services, but this did not account for differences in pollinator effectiveness. The decline in the abundance of orchid bees suggest that flowers that require those species with specially adapted tongue lengths, body sizes or mutual reationships based on fragrances are likely to be receiving fewer visits, and this could impact their reproduction and population viability and fruit set (which other animals may rely on). Furthermore, there may be changes in the community composition of pollinators, such as that detected in orchid bees, as well as changes in the

plant communities, as suggested by the vegetation structure data. These alterations in the community may led to changes in the plant-pollinator network interactions (Vázquez & Simberloff 2003), and changes in these complex networks could negatively impact both plant and insect species, as well as other components of the food web. Other studies have found that pollinations is negatively affected by forest disturbance (Klein, Steffan-Dewenter & Tscharntke 2003; Blanche, Ludwig & Cunningham 2006; Haddad *et al*. 2015), but these mainly focus on pollination of crop plants, and more studies of the impacts of disturbance on the pollination of native rainforest flora are needed.

In this study, I chose to consider disturbance rank as a continuous variable. I felt that this was the best way of recognising that the different land use types fell along a gradient of disturbance intensity, and that other intermediate disturbance levels could exist between them. I validated my choice of disturbance rank using vegetation structure data, and in order to use a truly continuous variable, I could have potentially used the vegetation principal component scores to represent disturbance rank. However, I felt that the vegetation structure scores were more difficult to relate to direct land uses, unlike the disturbance ranks, and vegetation structure could differ for other reasons not of interest in this study, such as in treefall gaps or river edges. This choice did have some limitations, as I could not know the exact spacing between my chosen disturbance levels, only that rank 1 was more disturbed than rank 2. Therefore, I used Spearman rank correlation tests in the analysis as the primary source of my conclusions regarding the relationship between diversity and disturbance, as this test requires only that the order of the disturbance ranking is correct, and the exact spacing is not an issue. Another alternative would have been to use an ordered discrete variable, but this would have required more data to fit. However, the simple approach used was supported by the vegetation data and while there is a risk that this was a less statistically powerful method and may have reduced my power to detect existing patterns, it does mean I can be reasonably confident in those patterns that were detected. A similar issue exists with the spatial structure of my sampling design; despite my efforts to intersperse the sites as much as possible, the reality was that more disturbed sites will almost always exist in the most accessible areas – in this case, on the east of the river, where the road and town are within easy access. I used

Moran's I tests to check for spatial autocorrelation in my models for all the datasets and was reassured to find that there were no issues (except a handful of very low, inconsistent correlations found in the butterfly data). I potentially could have included spatial variables in the models to remove any effect, but I was concerned that the east-west coordinates were too closely related to the disturbance gradient. I also considered analysing each side of the river separately, which would have removed this issue, but I did not have enough sites to be able to do this. Other options include the use of partial Mantel tests to quantify the contribution of geographic location and disturbance level or using GLMMs to account for the nested study design, which may be explored in future work.

7.3 Impact

The results of the studies presented in this thesis have some important consequences for biodiversity assessments. I hope that my work can inform future research in tropical forests by providing evidence of how a combination of biodiversity measures can be used to maximise the information available for biodiversity and conservation assessments, including demonstrations of the utility of similarity-sensitive diversity, which has not been widely adopted before now, and by raising awareness of the extent to which different patterns may be detected depending on the indices and taxa chosen. I have identified a need for clearer specification of biodiversity research aims and a selection of indicators properly suited to address those. The danger of choosing a single index for biodiversity assessment has been clearly illustrated and I recommend that future studies on the impacts of human disturbance on biodiversity are explicit in their choice of measure and preferably consider more than one index of diversity, including both alpha and beta perspectives. As I have found acoustic diversity to show unexpected and unintuitive patterns in response to human disturbance as well as to artificial layering of recordings, I would encourage people to continue studying natural soundscapes and their responses to disturbance, but to interpret the results with caution and avoid using them as the basis for important land management and conservation decisions unless considered alongside more established biodiversity approaches.

Incorporating multiple diversity measures into ecological assessments will provide land managers with more evidence on which to base their decisions. If several sources of evidence agree, the managers can have greater confidence in their decision. Where there are contradictory patterns, this can indicate the need for more detailed exploration of species patterns and flag up that this is an area for cautious decision making and careful prioritisation. I found a general improvement in biodiversity with less intensive land use, including agroforestry and regenerating forest. This supports a shift from open monocultures and encourages the use of agroforestry practices for the benefit of biodiversity and ecosystem functioning, as well as ecosystem service benefits to farmers. The higher biodiversity in regenerating forest compared to agricultural areas is also encouraging for managers dealing with areas of abandoned land, as under suitable conditions these areas can recover to make an important contribution to biodiversity and function (Whitworth *et al*. 2016b). However, minimally disturbed, old-growth forests remain of special importance for biodiversity, with unique species and complex communities that may not be fully recovered in regenerating secondary forest. Care should be taken to prioritise undisturbed forest for conservation, alongside the recovery of abandoned land and improvements to agricultural practices. Indicator taxa may be useful for monitoring the progress of forest regeneration and conservation efforts or detecting the impacts of disturbance on biodiversity, but these indicator groups should be used with caution. I would recommend using a combination of multiple taxa, and multiple diversity measures for each to get an impression of how biodiversity might be responding to conservation efforts or disturbance, and also consider how direct measures of some types of impacts, such as changes in vegetation structure, may be easier to measure directly without the use of indicators. I think that relationship between indicator groups and ecosystem functions is of high interest and should be considered when trying to understand the wider effects of disturbance and restoration efforts, but currently there is not enough evidence as to how the different species and functions interact, or to quantify the strength of the relationships for many groups.

Due to the way in which regional gamma diversity can be decomposed into alpha and beta components, one way of maximising gamma diversity is to promote high beta diversity between subcommunities. In some cases, this fits in well with

our instinctive sense of what makes a valuable habitat, such as a rainforest with complex microhabitats, including streams, tree-fall gaps, different canopy levels, rotting wood and large emergent trees at occasional intervals. This complexity is likely to result in a high beta diversity for many taxa, as they are adapted to these microhabitats within the forest, and this feels like a desirable forest condition to strive for. However, beta diversity can also be high in a matrix of different land uses, such as the gradient used in this study and, if used poorly, this result could be used to argue that regional diversity would be maximised by prioritising a matrix of land uses over contiguous pristine forest (Socolar *et al.* 2016), despite the alpha diversity and community composition of the disturbed sites indicating that they are individually of low conservation value. This dilemma could be an issue where a habitat-based approach is used to identify conservation priorities, with the aim of conserving a wide range of habitat types to maximise biodiversity (Hughes *et al.*, 2000). The habitat approach could efficiently protect a wide range of species without knowledge of their individual habitat preferences, but depending on how it is used, it could also result in favouring matrices including agriculture and secondary forest over contiguous areas of primary forest. These issues highlight the need for carefully selected and clearly-defined conservation goals, identifying what it is we are trying to achieve and how success will be measured.

7.4 Future research

In retrospect, I would have liked to have done more extensive work on the ecosystem functioning aspects of this research, as I found it very interesting to not only explore the patterns of biodiversity in response to disturbance, but to be able to place this in the context of what implications these might have for the functioning and resilience of the forest. I was keen to understand more about how the physical roles of dung beetles in the ecosystem affect soil quality, as this is an important basis for plant establishment in both agricultural and natural settings. Previous studies have shown that dung beetles make an important contribution to soil quality through aeration and the incorporation of nutrients, but my soil studies were quite limited, and more extensive sampling to directly link soil quality to differences in dung beetle activity at the dung arenas would have been better, as opposed to the more general connection made at the site level; unfortunately, this was not feasible due to time and

funding constraints. I also had hoped to use the Tea Bag Index (Keuskamp *et al.* 2013) as a measure of decomposition rates across the gradient to be included as part of the soil assessment. The simplicity and transferability of this method holds much appeal, including the ease with which it can provide information on the chemical and microbial properties of the soil, which could change as an indirect response to changes in dung beetle functions; unfortunately, I discovered this method too late to incorporate it into the fieldwork plan.

Using artificial flowers to compare pollinator visitation rates as a proxy for pollination potential was a promising approach, but the experimental design was very basic. A slightly expanded version could have added more information by recording the types of pollinators visiting, at a family level (bees, flies, butterflies etc.), as used in the new UK pollinator monitoring scheme (Centre for Ecology and Hydrology 2018). There is a trade-off between developing experiments to capture as much useful information as possible whilst keeping the experiments simple enough for rapid assessments and reliable performance by inexperienced volunteers. It would have been interesting to learn more about the pollination being performed by orchid bees and whether there was any change in the species or number of flowers pollinated across the gradient. Studies on orchid bees captured with pollinaria have shown what plants they visit (Roubik & Hanson 2004), and it would have be interesting to collect the pollen from the bees captured in difference sections of the gradient, to gather evidence about which plants they visit or the proportion of bees with pollinaria across the gradient. However, although of great interest, this would be time consuming and require considerable expertise in pollen identification, which was not available.

I found some interesting results of functional groups in the dung beetle study, with larger beetles appearing to be more sensitive to disturbance. It was hoped that there would be a chance to explore similar data with the orchid bees. The plan was to collect data on body size and tongue length, since those are key factors in what flowers they can access. However, time with the specimens was limited and identification had to be prioritised, which took longer than expected. Obtaining these data from the species descriptions in the literature was challenging, as it was difficult to find enough detailed information for all species, so this may be a topic to revisit in future. Body size of dung beetles also

sparked another idea, which was the effect of body size on dung detection and travel distance. The current standard trapping methodology (minimum 50m spacing between pitfall traps) is based on a detailed study that focused on the distances travelled by a single medium sized species (Larsen & Forsyth 2005). I hypothesised that larger beetles would be attracted from much further afield during the sampling period and attempted to test this. I captured dung beetles in non-lethal pitfall traps and then split them into size classes. I created equal-sized groups of beetles with representatives from each size class and marked them with nail polish of assorted colours to indicate the release distance. These groups were then released at set distances from a lethal baited pitfall trap, to see from what distances I recaptured each size of beetle. This was a very interesting pilot study, and I had a few individuals recaptured from beyond the 25m recommended trapping radius (Figure 7.2). This is an important result, because it provides evidence that the current recommendation of 50m between traps may not be sufficient for the traps to be independent samples. Our sample size was far too small for any real conclusions, but I think it would be valuable to further investigate the ideal trap spacing when a range of species are considered.

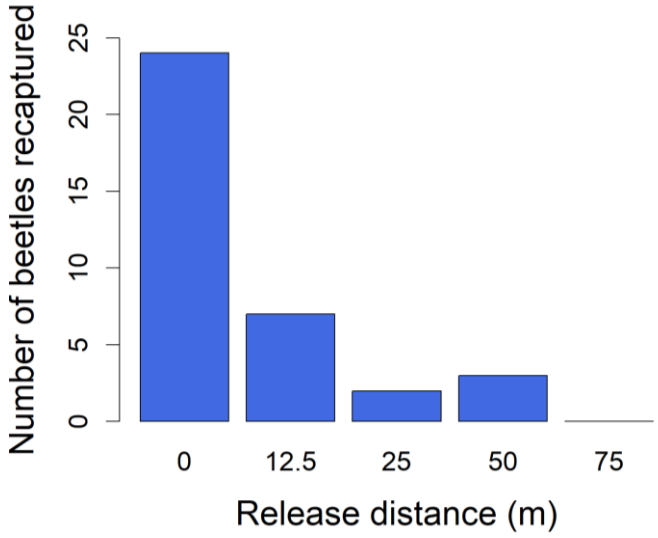

Figure 7.2 Dung beetles (of mixed sizes) recaptured at set release distances from a baited pitfall trap after 24 hours. Some individuals were recaptured from beyond the 25m distance recommended for independent trap spacing, suggesting this may need further testing.

A similar issue regarding attraction distance exists for orchid bees (Nemésio 2012): we still do not know the attraction distance of the baits, or how these differ between bait types or vegetation structures, where humidity, wind and evaporation may affect odour dispersion. Until this is investigated further,

identifying suitable distances between sampling will continue to be based on assumptions and estimates. One way of measuring attraction distance could be by capturing bees and then releasing them at different distances from a bait, as for the dung beetles, but it would be challenging to get suitable sample sizes and recapture rates might be very low. Other options include using trained detection dogs (Cablk *et al*. 2008) or electronic 'noses' (Brattoli *et al*. 2011), but neither of these options is readily available at present. Detectability distances were also an issue in the acoustics work, as I could not determine if there was any significant difference in audio transmission between our different vegetation types in the different disturbance levels. This could have been tested by using playback of sounds of a range of frequencies at set distances from the recorder and assessing at what distance those sounds could be detected and how this varied between habitats. This was partially attempted, but the quality of speakers available was inadequate for realistic playback, and there was not time to repeat it the following field season.

7.5 Contributions and gaps remaining

The differences in performance between diversity indices has been a topic that has attracted attention in recent literature (Morris *et al*. 2014; Socolar *et al*. 2016; Santini *et al*. 2017; Yoccoz, Ellingsen & Tveraa 2018). Despite a long history of attempts to quantify biodiversity, we still do not understand enough about how the various indices work for detecting different types of change in biological communities. This is an important matter to resolve if we want to effectively monitor the responses of biological communities to environmental change, which is an essential step in enabling us to conserve natural ecosystems and the services they provide (WWF 2016). Advances in soundscape ecology have provided an exciting novel approach to monitoring biodiversity, but there remains a lot of uncertainty as to which acoustic indices are appropriate under different circumstances. Currently, the ratio of new acoustic indices to papers published is very high (Sueur *et al*. 2014b), and I counted at least 23 different indices used in the papers cited in Chapter 6. We need more extensive testing of how these acoustic indices respond to distinct types and combinations of sound, and under a range of conditions, especially tropical forest environments. This could include creating artificial soundscapes with known combinations of species, including multiple taxonomic groups, as currently most studies focus on

birds, and then testing how well different indices can detect the diversity of species included in the recordings. Another important step would be to conduct soundscape recordings in tropical forest areas that have been extensively inventoried and compare how well the acoustic indices can distinguish between forests with different levels of diversity and different dominant groups (e.g. areas with high insect or frog activity, and high and low anthropogenic disturbance). There also remains a lot to learn about the relationship between biodiversity and ecosystem functioning, including how various types of diversity contribute to functioning, the relative importance of the various biological and geochemical components of the ecosystem and how interactions between species might increase or decrease functioning levels.

In this thesis, I have made a contribution towards filling some of these knowledge gaps, whilst others remain areas I would be interested in exploring more in future. I have provided evidence that whilst all the taxa I studied responded negatively to disturbance, their responses were not consistent and the most sensitive diversity measures for detecting the response depended on the group studied. Based on this, I have argued for biodiversity assessment to apply multiple measures, including alpha and beta indices, to avoid missing important patterns that could have implications for conservation and ecosystem functioning, and this is broadly relevant for ecological assessments worldwide. I have demonstrated how some new additions to the biodiversity toolkit can add useful insights into how communities respond to disturbance, including new measures of beta diversity (redundancy and representativeness) and the use of similarity sensitive-diversity indices. I have shown how biodiversity declines can impact ecosystem functioning in this neotropical forest disturbance gradient, at least in the case of dung beetles and the functions they provide, and I would like to see this explored further for other groups and types of functions. I have also shown that although soundscape diversity can provide an interesting angle for biodiversity assessment, the results are not as predictable as might be expected and do not clearly correlate with standard biodiversity inventory data. We therefore need a better understanding of how the acoustic diversity indices work to be able to use them confidently for conservation decision making. Overall, more generally, I have added to the evidence that human disturbance negatively impacts biodiversity, and that minimally disturbed tropical forests are of key

4117 importance for conservation. The evidence presented here also shows that the
4118 impact of human disturbance in this region has the potential to be somewhat
4119 reduced through improvements in small-scale agriculture and allowing degraded
4120 land to regenerate, alongside the strict protection of high-quality forest in the
4121 area.

8 Supplementary materials

8.1 Chapter 2

8.1.1 Tables

Table S3.2 – Vegetation structure data from all sites across the gradient. Three vegetation plots of 25m^2 were surveyed in each site, and multiple measures collected in each plot, depending on the variable, as described in Chapter 2, section 2.3.3.1. Data presented here are the mean values for each plot. DBH = diameter at breast height. Leaf litter depth was collected from 16 random points within the plot, and the frequency of herbs, bare ground and woody debris is the number of occasions when our leaf litter sample point coincided with any of these features (i.e. if the ruler touched them). Shrub and herb density were measured at four points using a modified Braun-Blanquet scale.

Disturbance rank	Site	Plot	Canopy height m	Canopy cover %	Mid-canopy height m	Mid-canopy cover %	Leaf litter depth mm	Mean DBH of 3 largest trees cm	Mean circumference of 3 largest trees cm	Count Trees >5cm DBH	Shrub layer density	Herb layer density	Freq. Herbs	Freq. Bare ground	Course woody debris
1	BA-A	1	4	0	0	28	41.25	2.76	8.67	1.00	4.00	5.50	3	0	2
1	BA-A	2	0	0	3	8.75	36.88	1.59	5.00	0.00	4.25	4.75	6	1	5
1	BA-A	3	0	0	2.5	23	76.31	7.64	24.00	1.00	6.00	1.25	9	0	4
1	BA-B	1	14	3	6	20	47.19	6.58	20.67	2.00	5.25	4.50	9	4	1
1	BA-B	2	12	2.5	4	2.5	39.69	1.91	18.00	1.00	5.50	5.75	13	3	0
1	BA-B	3	16	12.4	5	20	37.81	3.71	11.67	0.00	4.25	5.75	11	5	1
1	BA-C	1	5	0	3	4	139.33	60.00	0.00	0.00	0.00	3.25	0	0	0
1	BA-C	2	14	1	4	1	61.43	30.00	0.00	0.00	0.00	2.40	0	12	0
1	BA-C	3	12	17	1	3	72.97	102.00	0.00	0.00	0.00	3.00	0	4	0
2	AF-A	1	14	62	9	29	83.13	21.12	66.33	4.00	2.25	3.25	6	0	1
2	AF-A	2	14	34	7	11	44.69	1.06	3.33	0.00	3.00	4.00	5	0	6
2	AF-A	3	12	15	6	10	75.00	0.53	1.67	0.00	3.25	6.00	10	0	3

Disturbance rank	Site	Plot	Canopy height m	Canopy cover %	Mid-canopy height m	Mid-canopy cover %	Leaf litter depth mm	Mean DBH of 3 largest trees cm	Mean circumference of 3 largest trees cm	Count Trees >5cm DBH	Shrub layer density	Herb layer density	Freq. Herbs	Freq. Bare ground	Course woody debris
2	AF-B	1	15	8	7	40	23.31	14.64	69.00	2.00	4.50	6.00	11	6	2
2	AF-B	2	17	37	8	44	44.69	1.75	5.50	0.00	4.50	5.00	11	1	0
2	AF-B	3	15	7	7	60	19.50	12.41	39.00	2.00	5.25	5.25	10	2	0
2	AF-C	1	17	6	7	26	26.00	120.00	0.23	0.73	0.00	5.50	0	12	1
2	AF-C	2	14	9	5	12	26.00	80.00	11.35	35.67	0.00	5.00	0	10	3
2	AF-C	3	18	1	6	64	34.07	20.00	2.51	7.90	1.00	4.75	0	11	3
3	SF-A	1	9	29	7	56	33.75	8.06	25.33	9.00	5.75	3.25	4	0	2
3	SF-A	2	6	32	4	60	58.75	9.34	29.33	10.00	6.00	3.75	6	0	2
3	SF-A	3	10	38	6	62	74.06	10.72	33.67	11.00	5.25	2.25	4	0	1
3	SF-B	1	13	34	6	37	45.94	5.52	17.33	1.00	4.75	3.75	5	0	2
3	SF-B	2	11	33	8	23	69.06	14.32	45.00	7.00	3.50	3.00	7	0	3
3	SF-B	3	14	36	10	31	63.13	10.61	33.33	5.00	5.50	4.25	7	0	3
3	SF-C	1	12	49	8	52	57.37	50.00	21.65	68.00	6.00	5.25	0	2	1
3	SF-C	2	16	56	9	82	63.37	30.00	10.08	31.67	2.00	5.75	0	3	0
3	SF-C	3	17	26	8	84	70.00	70.00	21.86	68.67	4.00	5.75	0	4	0
4	CCR-A	1	12	60	9	64	55.44	21.54	67.67	8.00	4.75	5.00	3	6	2
4	CCR-A	2	13	18	8	67	51.38	20.05	63.00	9.00	5.50	5.25	8	7	0
4	CCR-A	3	11	26	9	90	66.50	12.52	39.33	8.00	5.50	5.25	6	2	1
4	CCR-B	1	15	68	12	54	70.81	15.60	49.00	7.00	5.25	5.50	7	0	4
4	CCR-B	2	14	44	10	60	70.38	7.75	24.33	7.00	6.00	5.75	7	2	0
4	CCR-B	3	18	62	9	72	65.31	27.38	86.00	8.00	5.67	5.67	4	2	1
4	CCR-C	1	12	82	9	46	58.69	20.06	63.00	7.00	5.50	4.50	10	1	5
4	CCR-C	2	12	26	8	72	53.19	11.14	35.00	9.00	5.00	6.00	11	0	4
4	CCR-C	3	10	58	8	58	58.31	26.74	84.00	7.00	5.50	5.25	5	0	4

Disturbance rank	Site	Plot	Canopy height m	Canopy cover %	Mid-canopy height m	Mid-canopy cover %	Leaf litter depth mm	Mean DBH of 3 largest trees cm	Mean circumference of 3 largest trees cm	Count Trees >5cm DBH	Shrub layer density	Herb layer density	Freq. Herbs	Freq. Bare ground	Course woody debris
5	MXD-A	1	15	74	9	40	71.88	29.50	92.67	19.00	5.00	5.00	6	0	4
5	MXD-A	2	17	40	9	58	80.29	16.76	52.67	18.00	5.25	5.75	8	0	5
5	MXD-A	3	15	33	10	70	38.69	8.17	25.67	1.00	5.50	5.00	6	0	5
5	MXD-B	1	20	50	14	54	23.60	45.00	12.42	39.00	5.00	5.75	0	7	4
5	MXD-B	2	24	74	12	44	25.93	0.00	20.27	63.67	9.00	5.00	0	7	2
5	MXD-B	3	17	58	9	50	18.27	0.00	20.90	65.67	7.00	5.50	0	6	3
5	MXD-C	1	17	48	14	66	62.69	26.10	82.00	6.00	5.00	5.50	11	0	2
5	MXD-C	2	18	52	15	42	68.38	41.07	129.00	6.00	5.25	5.50	11	0	8
5	MXD-C	3	17	60	14	64	66.63	33.85	106.33	8.00	5.50	5.50	0	0	0
6	MIN-A	1	26	68	18	60	78.56	63.35	199.00	12.00	3.75	3.50	4	0	5
6	MIN-A	2	20	66	15	68	32.75	19.52	61.33	7.00	3.25	3.00	6	2	3
6	MIN-A	3	22	72	18	56	53.19	43.82	137.67	10.00	3.75	3.75	3	0	4
6	MIN-B	1	28	81	15	66	34.07	41.00	30.77	96.67	11.00	2.75	0	4	0
6	MIN-B	2	29	74	16	72	41.60	12.00	13.26	41.67	11.00	3.00	0	5	1
6	MIN-B	3	22	70	14	52	34.00	0.00	15.70	49.33	5.00	4.00	0	6	3
6	MIN-C	1	32	74	22	88	21.25	25.15	79.00	9.00	4.00	4.00	13	9	1
6	MIN-C	2	24	54	14	58	69.19	43.72	137.33	10.00	3.50	3.00	7	0	3
6	MIN-C	3	23	74	17	70	36.44	16.77	52.67	7.00	2.75	2.75	6	0	1

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8.2 Chapter 3

8.2.1 Figures

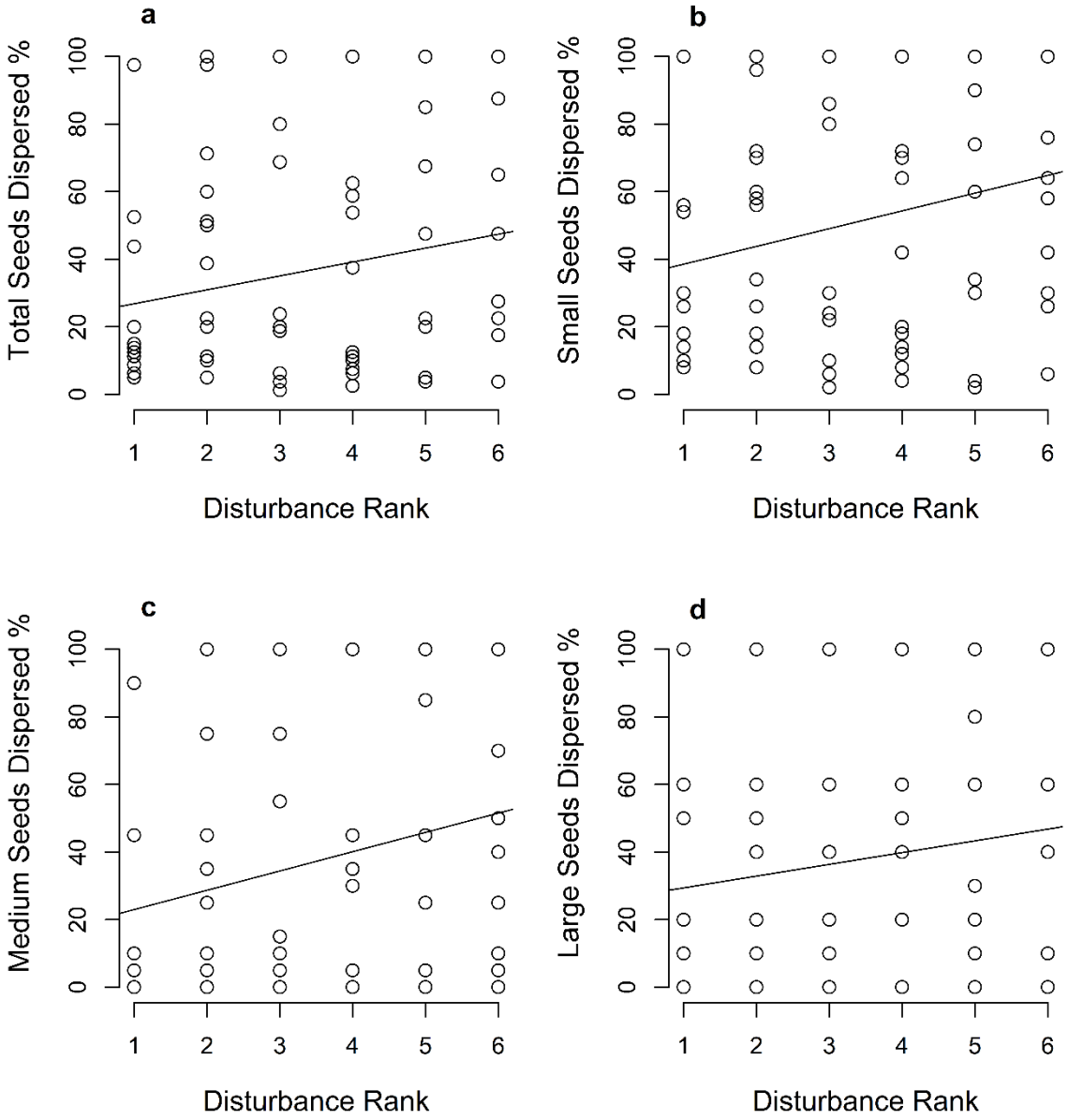

Figure S3.1 Ecosystem functions in response to disturbance. The percentage of a) small seeds dispersed, (b) medium seeds dispersed, (c) large seeds dispersed, and (d) the percentage of dung removed. Disturbance rank goes from 1 = most disturbed to 6 = least disturbed.

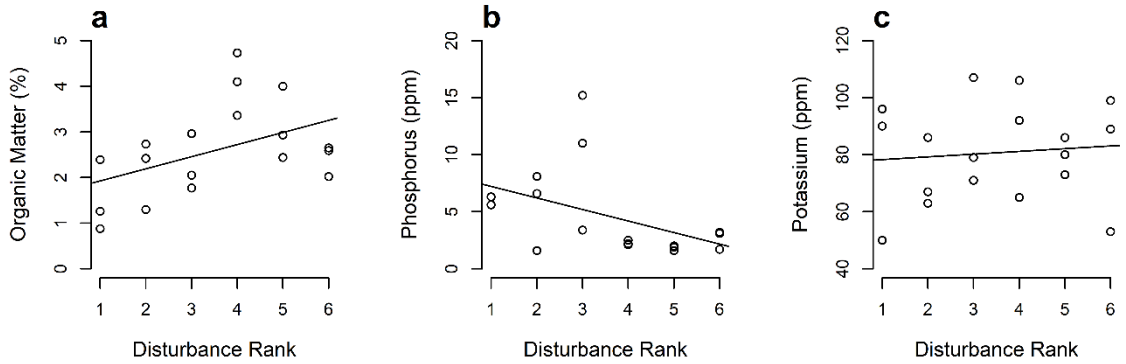

Figure S3.2 Changes in soil nutrient levels in response to disturbance. The levels of (a) soil organic matter, (b) phosphorus and (c) potassium detected along the disturbance gradient. Disturbance rank runs from 1 (most disturbed sites) to 6 (least disturbed), with a line indicating the linear relationship between the x and y variables.

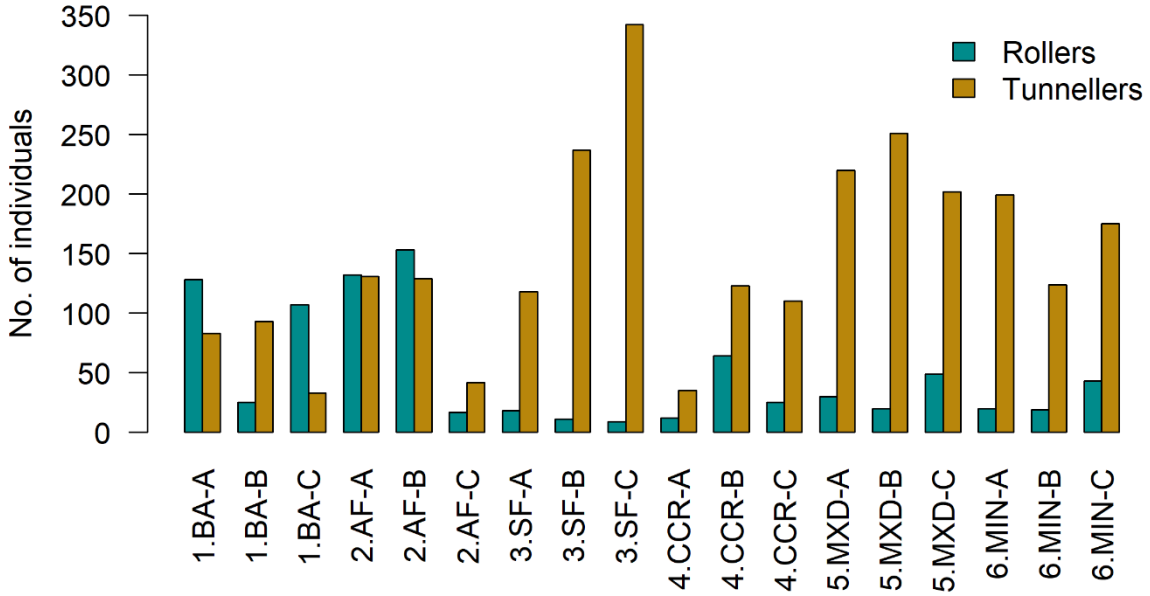

Figure S3.3 Abundance of rollers (blue bars) and tunnellers (gold bars) at each site across the gradient. The sites are labelled with their disturbance rank, habitat abbreviation and replicate group (a, b or c).

4149 ## 8.2.2 Tables

4150

4151 Table S3.1 Summary of previous dung beetle research. Includes a selection of the most relevant studies on dung beetle diversity in response to human disturbance,
4152 including the measures used and key findings.

Study	Location	Habitats compared	Measures used	Response
Audino et al. (2014)	Atlantic forest, Brazil	Forest restoration of varying ages (0-18 years) compared to primary forest (PF) and old secondary forest (>40 years old: SF) reference sites, and degraded pastures.	Species richness (observed)	Highest richness in PF and SF, lowest in new restoration areas, intermediate in mid/late stage restoration.
			Species richness (rarefied)	No significant difference.
			Abundance	Highest abundance in PF and SF.
			Biomass	Biomass increased with forest age, highest in PF and SF.
			Species composition (similarity to reference sites)	Percentage of forest specialist species increased with forest age.
			Functional richness	Functional richness highest in PF and SF.
Barragán et al.(2011)	Mexico	Rainforest and scrub compared to pasture.	Functional diversity (rollers/tunnelers, body size, diurnal/nocturnal, diet)	Functional richness higher in less disturbed habitat. Large, paracoprid, nocturnal coprophages were the most sensitive to habitat conversion.
Braga et al. (2013)	Amazon, Brazil	Gradient: primary forest, secondary forest (<15 years old), agroforest, small-scale slash and burn agriculture, pasture.	Species richness (observed)	Decreased with increased land use intensity.
			Abundance	Decreased with increased land use intensity.
			Biomass	Decreased with increased land use intensity.

			Body size	Richness and abundance of large beetles decreased with increased land use intensity. Small beetles showed no change in abundance but had higher richness in primary forest.
Nichols et al. (2013)	Neotropics and Afro-Eurasian tropics	Gradient of canopy openness: primary forest, selectively logged/regenerating forest, agroforestry and open agriculture	Body mass (abundance of large/small)	Abundance of large beetles increased with increased intensity of forest conversion.
			Roller/tunneller abundance	Roller species suffered greater declines than tunnellers in agroforestry but had moderately higher abundances in open agriculture.
			Diurnal/ nocturnal abundance	Nocturnal species declined more severely than diurnal
			Abundance (overall)	Declined with loss of forest cover.
Nichols et al. (2007)	Global	Intact forest compared to selectively logged forest, secondary forest, agroforestry, agriculture and pasture and clear cuts.	Species richness	Declined compared to intact forest for all disturbance types, with increased loss of richness with increased disturbance intensity.
			Abundance (total)	Only communities in clear-cut areas significantly declined relative to intact forest. Where abundance showed little changed, the more disturbed habitats were often characterized by a hyper abundance of small bodied species.
			Abundance of forest species	Abundance of intact forest species significantly declined in early secondary forest, agriculture and clear-cut areas.
			Community evenness	Dung beetle community evenness declined relative to intact forest levels across most modified habitat types.

			Community similarity to intact forest	Dung beetle community similarity relative to intact forest declined below 0.85 in most modified habitats and reached nearly zero in tree-less habitats.
Barnes et al. (2014)	Nigeria	Gradient from intact forest to regenerating forest at forest edge, and degraded pasture at forest edge.	Abundance	Highest in forest, medium in regenerating forest, and lowest in pasture.
			Species richness	No difference between intact forest and regenerating forest, lower richness in pasture.
			Community similarity to intact forest	Regenerating forest had more similar communities to the intact forest than the pasture.
Horgan (2005)	Peru	Comparison between forested and deforested agricultural sites	Abundance	Highest in forested sites
			Species richness	Highest in forested sites
			Biomass	Highest in forested sites
Horgan (2009)	Peru	Comparison between forested and deforested agricultural sites (chacras with banana and other crops, shade coffee, regenerating forest, intact forest)	Abundance	No effect.
			Species richness	Higher in forest.
			Biomass	Higher in forest.
			Community similarity	Shade coffee and regenerating forest similar to intact forest; chacras distinct from shaded habitats.
Hayes et al. (2009)	Vietnam	Continuous gradient of disturbance, including primary forest, regenerating forest and agriculture.	Species richness (Chao 2 estimate)	No relationship with disturbance.
			Fisher's Alpha	Increase in diversity with disturbance.
			Rollers/tunnellers	The richness of roller species was significantly lower in more disturbed sites, but there was no relationship between disturbance and tunneller species richness.
Davis and Philips (2009)	West Africa	Primary rain forest, selectively logged forest, plantations, deciduous forest and disturbed open savannah.	Species composition	Similarity of species composition high between primary and selectively logged forest, much lower similarity between primary forest and plantation or savannah.

Slade et al. (2011)	Malaysian Borneo	Undisturbed forest, selectively logged forest and intensively logged forest.	Observed species richness	No response to logging intensity
			Rarefied species richness	Lower richness in intensively logged forest. High richness in selectively logged.
			Abundance	No response to logging intensity
			Biomass	No response to logging intensity
			Species composition	There was low species turnover among sites
			Guild structure	No trend.
			Dung removal	Less dung removed in intensively logged sites. Correlated positively with species richness and with the biomass of large nocturnal tunnelers
			Proportion of seeds removed	Fewer seeds removed in intensively logged sites. Small seeds removed more than larger seeds.
Scheffler, (2005)	Brazilian Amazon	A mosaic of intact forest, selectively logged forest, second-growth forest, and forest clear cuts in a surrounding matrix of cattle pasture.	Beetles size (weight and length)	Beetles in clear cuts and pasture were smaller than those in intact or selectively logged forest.
			Species richness	Highest in intact forest, then selectively logged, clear cut and lowest in pasture.
			Shannon diversity	Highest in intact forest, then selectively logged, clear cut and lowest in pasture.
			Simpson diversity	Highest in selectively logged, then intact, clear cut and lowest in pasture.
			Abundance	Much higher in pasture.
			Species composition	Intact and selectively logged forest similar, distinct communities in pasture and clear cut.
			Biomass	Lowest in clear cut, highest in pasture (small beetles).
Vulinec (2002)	Brazilian Amazon	Primary forest, secondary growth, and clear-cuts	Abundance	No difference between primary and secondary growth but clear-cut lower.
			Species richness	No difference between primary and secondary growth but clear-cut lower.

			Species composition	Different community found in clear cuts compared to second growth and primary. Rollers and diurnal species seem more abundant in primary forest.
Rös et al. (2012)	Mexico	Cloud forest, secondary forest, low vegetation (including crops) and pasture	Species richness	Lowest in cloud forest, and highest in secondary
			Abundance	Lowest in low vegetation, highest in pasture.
			Shannon diversity	Lowest in cloud forest, highest in low vegetation, followed by pasture and secondary.
			Biomass	Lowest in low vegetation, highest in pasture.
			Individual beetle biomass	Cloud forest highest, pasture lowest
Cajaiba et al. (2017)	Brazilian Amazon	Natural forest, mature secondary forest, early secondary forest, agriculture and pasture	Species richness	Highest in natural forest, then mature secondary, similarly low in all more disturbed sites.
			Abundance	Highest in natural forest, then mature secondary, low in more disturbed habitats.
			Shannon diversity	Highest in natural forest, then mature secondary, and early secondary, lowest in agriculture and pasture.
			Berger-Parker dominance	Highest in agriculture and pasture, then secondary forest, and lowest in natural forest.
			IndVal indicator species	Of 112 species sampled, 23 species were significantly associated with natural forest, eight with pasture, and six with early secondary forest.

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Table S3.2 List of dung beetles species found in this study.

Species
Anisocanthon villosus
Ateuchus connexus
Canthidium basipunctatum
Canthidium bicolor
Canthidium copreum
Canthidium gerstaeckeri
Canthidium lentum
Canthon aequinoctialis
Canthon brunneus
Canthon fulgidus
Canthon luteicollis
Canthon monilifer
Canthon quinquemaculatus
Canthon septemaculatus
Canthon subhyalinus
Canthon virens
Coprophanaeus telamon
Cryptocanthon campbellorum
Deltochilum amazonicum
Deltochilum carinatum
Deltochilum granulatum
Deltochilum orbiculare
Deltochilum peruanum
Deltochilum sp. 16
Dichotomius batesi
Dichotomius conicollis
Dichotomius mamillatus
Dichotomius nr. lucasi
Dichotomius ohausi
Dichotomius prietoi
Dichotomius robustus
Dichotomius worontzowi
Eurysternus caribaeus
Eurysternus foedus
Eurysternus hamaticollis
Eurysternus hypocrita
Eurysternus lanuginosus
Eurysternus nigrovirens
Eurysternus plebejus
Eurysternus wittmerorum
Ontherus pubens
Onthophagus haematopus
Onthophagus onorei
Onthophagus osculatii
Onthophagus rhinophyllus
Onthophagus rubrescens
Onthophagus xanthomerus
Oxysternon conspicillatum
Oxysternon silenus

Oxysternon spiniferum
Phanaeus cambeforti
Phanaeus chalcomelas
Scybalocanthon aereus
Scybalocanthon nr. zischkai
Sylvicanthon bridarolli
Uroxys 1
Uroxys 2

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Table S3.3 Results of the Spearman rank correlation tests. The p and rho values of the results of correlations between variables 1 and 2 are shown for all tests. Where the correlation appeared significant, the results were bootstrapped to provide the 95% confidence interval for the rho values.

Variable 1	Variable 2	p	rho	rho 95% CI
Observed q0	Rank	0.0005	0.73	0.3739 - 0.9494
Observed q1	Rank	0.0302	0.51	0.1044 - 0.7748
Observed q2	Rank	0.2735	0.27	-0.2154 - 0.6578
Observed qInf	Rank	0.6467	0.12	-0.3711 - 0.5387
Vegetation Structure PC1	Rank	0.0000	0.91	0.7047 - 0.9741
Estimated q0	Rank	0.0106	0.59	0.0908 - 0.9071
Estimated q1	Rank	0.0753	0.43	-0.0033 - 0.7359
Estimated q2	Rank	0.2735	0.27	
Total abundance	Rank	0.8847	-0.02	
Small seeds dispersed	Temperature	0.0508	-0.23	
Small seeds dispersed	Rainfall	0.3828	-0.10	
Small seeds dispersed	Humidity	0.1805	-0.16	
Small seeds dispersed	Rank	0.0417	0.24	0.0272 - 0.4415
Medium seeds dispersed	Rank	0.0102	0.30	0.0813 - 0.5035
Large seeds dispersed	Rank	0.2390	0.14	
Dung removed	Rank	0.6804	0.05	
Roller Observed q0	Rank	0.0084	0.60	0.1590- 0.8659
Roller Observed q1	Rank	0.0078	0.61	0.1513 - 0.9266
Roller Observed q2	Rank	0.0218	0.54	0.0426 - 0.8754
Roller Observed qInf	Rank	0.0234	0.53	0.0551 - 0.8762
Tunneller Observed q0	Rank	0.0011	0.71	0.2767 - 0.9456
Tunneller Observed q1	Rank	0.0040	0.64	0.2342 - 0.8988
Tunneller Observed q2	Rank	0.0201	0.54	0.0860 - 0.8346
Tunneller Observed qInf	Rank	0.0753	0.43	-0.0501 - 0.7778
Roller Abundance	Rank	0.3212	-0.25	-0.5998 - 0.2799
Tunneller Abundance	Rank	0.3476	0.24	-0.2866- 0.7245
Small Observed q0	Rank	0.5134	0.16	
Small Observed q1	Rank	0.4625	0.18	
Small Observed q2	Rank	0.8724	0.04	
Small Observed qInf	Rank	0.8530	0.05	
Small Abundance	Rank	0.5099	-0.17	
Large Observed q0	Rank	0.0000	0.83	0.5293 - 0.9574
Large Observed q1	Rank	0.0078	0.61	0.1301 - 0.8875
Large Observed q2	Rank	0.0440	0.48	-0.0798 - 0.8215
Large Observed qInf	Rank	0.0579	0.45	-0.0831 - 0.8031
Large Abundance	Rank	0.3332	0.24	
Soil K	Rank	0.6919	0.10	
Soil Organic Matter	Rank	0.0472	0.47	-0.0211 - 0.7808

Variable 1	Variable 2	p	rho	rho 95% CI
Soil P	Rank	0.0175	-0.55	-0.8223 - -0.1333
q0 raw iNEXT estimates (x1000)	Rank difference	0.0002	0.82	
q1 raw iNEXT estimates (x1000)	Rank difference	0.0743	0.47	
q2 raw iNEXT estimates (x1000)	Rank difference	0.5455	0.17	
q3 raw iNEXT estimates (x1000)	Rank difference	0.5323	0.18	

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Table S3.4 Model selection including environmental variables. Where the correlations tested in Table S3.3 were significant, linear and mixed models were used to control for the effect of other environmental variables. The log likelihoods and degrees of freedom for all models tested are presented here, with the models divided into sections based on the response variables used.

Model	Log Likelihood	DF
Vegetation		
Vegetation Structure PC1 ~ Rank	-0.6351	3
Vegetation Structure PC1 ~ Rank + Elevation	-0.6153	4
Vegetation Structure PC1 ~ Rank + Distance to River	-0.3638	4
Vegetation Structure PC1 ~ Rank + Rain	1.0909	4
Diversity		
log(Observed q0) ~ Rank	5.9630	3
log(Observed q0) ~ Rank + Elevation	7.0171	4
log(Observed q0) ~ Rank + Distance to River	5.9691	4
log(Observed q0) ~ Rank + Rain	6.1337	4
log(Observed q1) ~ Rank	-6.8958	3
log(Observed q1) ~ Rank + Elevation	-6.8954	4
log(Observed q1) ~ Rank + Distance to River	-5.5089	4
log(Observed q1) ~ Rank + Rain	-6.3480	4
log(Observed q2) ~ Rank	-10.5628	3
log(Observed q2) ~ Rank + Elevation	-10.4479	4
log(Observed q2) ~ Rank + Distance to River	-9.3995	4
log(Observed q2) ~ Rank + Rain	-9.8493	4
log(Observed q3) ~ Rank	-10.4282	3
log(Observed qInf) ~ Rank	-6.2322	3
log(Observed qInf) ~ Rank + Elevation	-6.0452	4
log(Observed qInf) ~ Rank + Distance to River	-5.5283	4
log(Observed qInf) ~ Rank + Rain	-5.6927	4
log(Estimated q0) ~ Rank	4.9725	3
log(Estimated q0) ~ Rank + Elevation	5.5934	4
log(Estimated q0) ~ Rank + Distance to River	5.0675	4
log(Estimated q0) ~ Rank + Rain	5.0037	4
log(Estimated q1) ~ Rank	-8.3387	3
log(Estimated q1) ~ Rank + Elevation	-8.3229	4
log(Estimated q1) ~ Rank + Distance to River	-6.7365	4
log(Estimated q1) ~ Rank + Rain	-7.9522	4

Model	Log Likelihood	DF
log(Estimated q2) ~ Rank	-11.3065	3
log(Estimated q2) ~ Rank + Elevation	-11.1450	4
log(Estimated q2) ~ Rank + Distance to River	-10.0126	4
log(Estimated q2) ~ Rank + Rain	-10.7423	4
Functional Groups		
log(ROLLERObserved q0) ~ Rank	0.3096	3
log(ROLLERObserved q0) ~ Rank + Elevation	0.3216	4
log(ROLLERObserved q0) ~ Rank + Distance to River	0.3407	4
log(ROLLERObserved q0) ~ Rank + Rain	0.3993	4
log(ROLLERObserved q1) ~ Rank	-3.0368	3
log(ROLLERObserved q1) ~ Rank + Elevation	-2.9676	4
log(ROLLERObserved q1) ~ Rank + Distance to River	-3.0121	4
log(ROLLERObserved q1) ~ Rank + Rain	-2.9418	4
log(ROLLERObserved q2) ~ Rank	-3.8694	3
log(ROLLERObserved q2) ~ Rank + Elevation	-3.8400	4
log(ROLLERObserved q2) ~ Rank + Distance to River	-3.8682	4
log(ROLLERObserved q2) ~ Rank + Rain	-3.8421	4
log(ROLLERObserved qInf) ~ Rank	1.8601	3
log(ROLLERObserved qInf) ~ Rank + Elevation	1.8670	4
log(ROLLERObserved qInf) ~ Rank + Distance to River	1.9397	4
log(ROLLERObserved qInf) ~ Rank + Rain	1.8621	4
log(TUNNELLERObserved q0) ~ Rank	-1.2353	3
log(TUNNELLERObserved q0) ~ Rank + Elevation	0.0001	4
log(TUNNELLERObserved q0) ~ Rank + Distance to River	-1.2294	4
log(TUNNELLERObserved q0) ~ Rank + Rain	-0.7640	4
log(TUNNELLERObserved q1) ~ Rank	-6.9639	3
log(TUNNELLERObserved q1) ~ Rank + Elevation	-6.9492	4
log(TUNNELLERObserved q1) ~ Rank + Distance to River	-4.0129	4
log(TUNNELLERObserved q1) ~ Rank + Distance to River + Rain	-3.5563	5
log(TUNNELLERObserved q2) ~ Rank	-7.9159	3
log(TUNNELLERObserved q2) ~ Rank + Elevation	-7.6113	4
log(TUNNELLERObserved q2) ~ Rank + Distance to River	-5.0531	4
log(TUNNELLERObserved q2) ~ Rank + Distance to River + Rain	-4.4385	5
log(large_Observed q0) ~ Rank	-0.4620	3

Model	Log Likelihood	DF
log(large_Observed q0) ~ Rank + Elevation	-0.4386	4
log(large_Observed q0) ~ Rank + Distance to River	-0.4354	4
log(large_Observed q0) ~ Rank + Rain	0.6741	4
log(large_Observed q1) ~ Rank	-3.0142	3
log(large_Observed q1) ~ Rank + Elevation	-2.8282	4
log(large_Observed q1) ~ Rank + Distance to River	-2.9933	4
log(large_Observed q1) ~ Rank + Rain	-2.8526	4
Ecosystem Functions		
Proportion small seeds dispersed ~ Rank + (1|Site/Arena) + (1|Date_checked), family=binomial	-424.3656	5
Proportion small seeds dispersed ~ Rank + (1|Site/Arena) + (1|Date_checked) + (1|observation), family=binomial	-265.9113	6
log(Soil Organic Matter) ~ Rank	-6.9854	3
log(Soil Organic Matter) ~ Rank + Elevation	-6.7880	4
log(Soil Organic Matter) ~ Rank + Distance to River	-6.8740	4
log(Soil Organic Matter) ~ Rank + Rain	-6.9081	4
log(Soil P) ~ Rank	-15.0221	3
log(Soil P) ~ Rank + Elevation	-14.8757	4
log(Soil P) ~ Rank + Distance to River	-13.9459	4
log(Soil P) ~ Rank + Rain	-14.5310	4

4172 Table S3.5 Results of the best fitting models.
4173 The estimated coefficients and significance are presented for the explanatory variables found to
4174 produce the best fitting models identified in Table S3.4.

Model	Variable	Est. coefficient	SE	t	p
log(Observed q0) ~ Rank	Rank	0.099	0.025	3.91	0.001
log(Observed q1) ~ Rank	Rank	0.108	0.052	2.09	0.053
log(Observed q2) ~ Rank	Rank	0.070	0.064	1.10	0.286
log(Observed qInf) ~ Rank	Rank	0.025	0.050	0.50	0.628
Vegetation Structure PC1 ~ Rank	Rank	0.293	0.037	7.97	0.000
log(Estimated q0) ~ Rank	Rank	0.089	0.027	3.32	0.004
log(Estimated q1) ~ Rank	Rank	0.107	0.056	1.90	0.076
log(Estimated q2) ~ Rank	Rank	0.070	0.066	1.06	0.305
Proportion small seeds dispersed ~ Rank + (1|Site/Arena) + (1|Date_checked) + (1|observation), family=binomial	Rank	0.352	0.246	1.43	0.153
log(ROLLERObserved q0) ~ Rank	Rank	0.082	0.035	2.37	0.031
log(ROLLERObserved q1) ~ Rank	Rank	0.136	0.042	3.25	0.005
log(ROLLERObserved q2) ~ Rank	Rank	0.130	0.044	2.96	0.009
log(ROLLERObserved qInf) ~ Rank	Rank	0.097	0.032	3.05	0.008
log(TUNNELLERObserved q0) ~ Rank	Rank	0.129	0.038	3.41	0.004
log(TUNNELLERObserved q1) ~ Rank + Distance to River	Rank	0.181	0.047	3.85	0.002
	Distance to river	0.000	0.000	-2.41	0.029
log(TUNNELLERObserved q2) ~ Rank + Distance to River	Rank	0.165	0.050	3.31	0.005
	Distance to river	0.000	0.000	-2.37	0.032
log(large_Observed q0) ~ Rank	Rank	0.199	0.036	5.48	0.000
log(large_Observed q1) ~ Rank	Rank	0.176	0.042	4.21	0.001
log(Soil pH) ~ Rank	Rank	-0.053	0.013	-4.15	0.001
log(Soil Organic Matter) ~ Rank	Rank	0.130	0.052	2.50	0.024
log(Soil P) ~ Rank	Rank	-0.235	0.082	-2.89	0.011

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Table S3.6 Results of Moran's I test for spatial autocorrelation.
For all models where a significant correlation was found, a test of spatial autocorrelation was performed on the residuals.

Model	Observed	Expected	Obs - Exp	SD	p
log(Observed q0) ~ Rank	-0.236	-0.059	-0.177	0.093	0.056
log(Observed q1) ~ Rank	0.022	-0.059	0.081	0.091	0.370
log(Observed q2) ~ Rank	-0.029	-0.059	0.030	0.091	0.742
log(Observed qInf) ~ Rank	-0.037	-0.059	0.021	0.093	0.818
log(Vegetation Structure PC1) ~ Rank	-0.018	-0.059	0.041	0.096	0.667
log(Estimated q0) ~ Rank	-0.189	-0.059	-0.130	0.09	0.16
log(Estimated q1) ~ Rank	0.013	-0.059	0.072	0.09	0.43
log(Estimated q2) ~ Rank	-0.027	-0.059	0.032	0.09	0.73
log(ROLLERObserved q0) ~ Rank	-0.069	-0.059	-0.010	0.087	0.907
log(ROLLERObserved q1) ~ Rank	-0.317	-0.059	-0.258	0.092	0.005
log(ROLLERObserved q2) ~ Rank	-0.340	-0.059	-0.281	0.092	0.002
log(ROLLERObserved qInf) ~ Rank	-0.335	-0.059	-0.276	0.093	0.003
log(TUNNELLERObserved q0) ~ Rank	-0.178	-0.059	-0.119	0.092	0.197
log(TUNNELLERObserved q1) ~ Rank + Distance to River	0.046	-0.059	0.105	0.089	0.235
log(TUNNELLERObserved q2) ~ Rank + Distance to River	-0.008	-0.059	0.050	0.090	0.575
log(large_Observed q0) ~ Rank	-0.252	-0.059	-0.193	0.092	0.035
log(large_Observed q1) ~ Rank	-0.269	-0.059	-0.210	0.095	0.027
log(Soil pH) ~ Rank	-0.046	-0.059	0.013	0.093	0.886
log(Soil Organic Matter) ~ Rank	0.015	-0.059	0.074	0.095	0.437
log(Soil P) ~ Rank	0.016	-0.059	0.075	0.090	0.403

8.3 Chapter 4

8.3.1 Figures

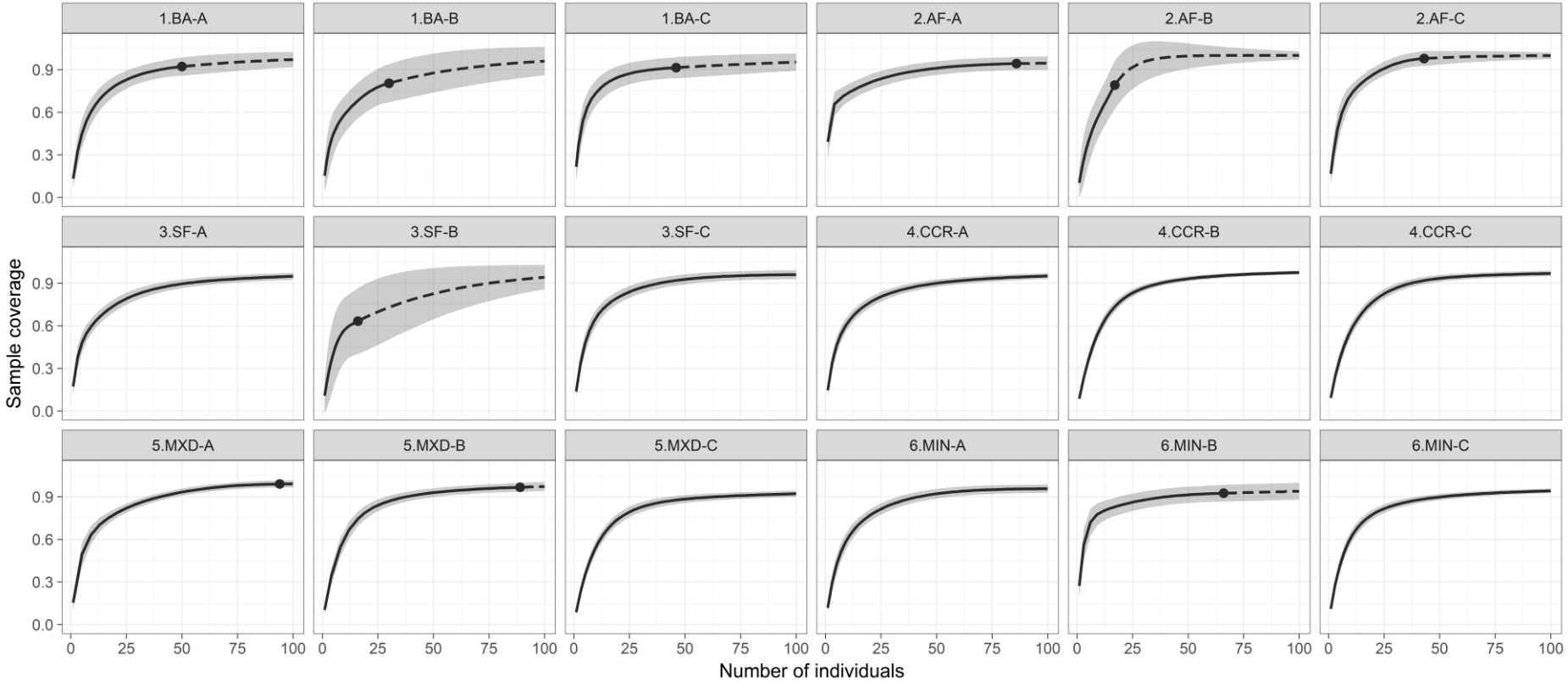

Figure S4.1 Sample completeness at q = 0. The sample completeness for each site is shown in a separate panel. The labels above each panel describe the disturbance rank (1-6, 1 is most disturbed) and habitat type of each site (BA: Banana, AF: Agroforestry, SF: Disturbed secondary forest, CCR: Cleared regenerating forest, MXD: Mixed history regenerating forest and MIN: minimally disturbed primary forest), as well as which of the replicates it was (A, B or C). The solid black line shows the rarefied estimate of sample coverage, and the dashed line is the extrapolated estimate, with the circle indicating the sample size collected. The grey shading indicates the 95% confidence interval around the coverage estimate. Coverage is shown up to 100 individuals for easy comparison between sites, but some sites did exceed this number; estimated diversity was compared at n = 50.

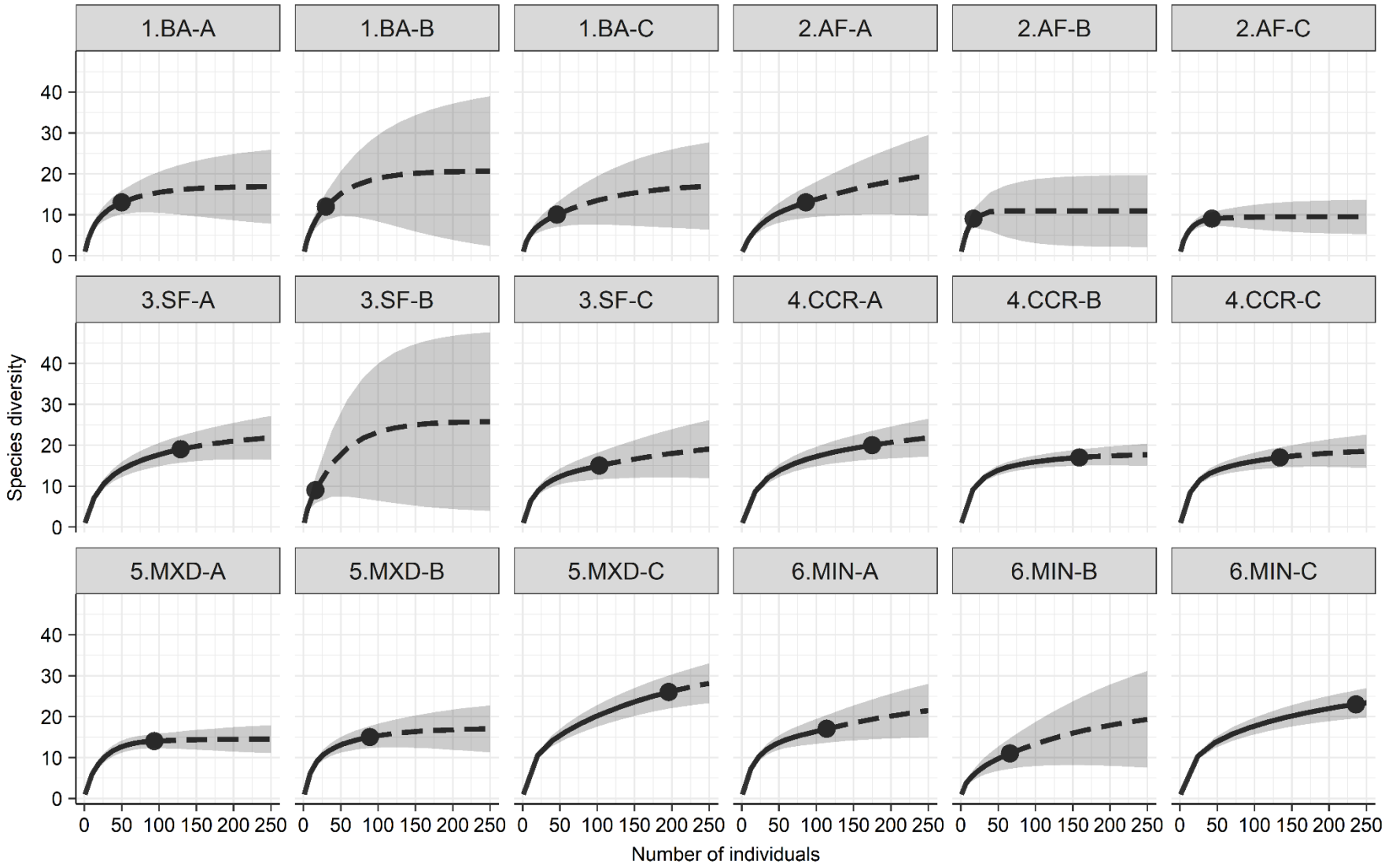

Figure S4.2 Estimated richness at each site extrapolated to a sample size of 250 individuals. Solid line shows rarefied estimate, dashed line shows extrapolation, and filled circle indicates the collected sample size. Shaded area indicates 95% confidence interval with 1000 bootstraps.

8.3.2 Tables

Table S4.1 Results of the Spearman rank correlation tests. The p and rho values of the results of correlations between variables 1 and 2 are shown for all tests, along with the 95% confidence interval for the rho values.

Variable 1	Variable 2	p	rho	rho 95% CI
Abundance	Disturbance rank	0.0051	0.6301	0.2534 - 0.8303
Observed diversity q = 0	Disturbance rank	0.0141	0.5672	0.1538 - 0.808
Observed diversity q = 1	Disturbance rank	0.0302	0.5110	0.0105 - 0.8576
Observed diversity q = 2	Disturbance rank	0.0581	0.4546	-0.0517 - 0.817
Observed diversity q = ∞	Disturbance rank	0.0801	0.4232	-0.0701 - 0.7895
Vegetation structure PC1	Disturbance rank	0.0000	0.9248	0.7517 - 0.9796
Estimated diversity q = 0 (mean)	Disturbance rank	0.4472	0.1912	-0.3512 - 0.6686
Estimated diversity q = 1 (mean)	Disturbance rank	0.3747	0.2226	-0.2824 - 0.622
Estimated diversity q = 2 (mean)	Disturbance rank	0.2300	0.2978	-0.1826 - 0.6794
q = 0 raw iNEXT diversity estimates (x1000)	Difference in disturbance rank	0.3318	0.2693	-0.2551 - 0.6685
q = 1 raw iNEXT diversity estimates (x1000)	Difference in disturbance rank	0.3782	0.2453	-0.295 - 0.6639
q = 2 raw iNEXT diversity estimates (x1000)	Difference in disturbance rank	0.4201	0.2250	-0.3067 - 0.6463
Redundancy (ρ) q = 1	Disturbance rank	0.0168	-0.5549	-0.7938 - -0.1434
Representativeness (ρ) q = 1	Disturbance rank	0.0380	0.4922	0.0075 - 0.8126
Pollinator visits	Disturbance rank	0.6467	0.1160	-0.3499 - 0.5397
Pollinator visits	Observed diversity q = 0	0.4380	-0.1950	-0.5965 - 0.2459
Pollinator visits	Observed diversity q = 1	0.4331	-0.1971	-0.6293 - 0.3067
Pollinator visits	Observed diversity q = 2	0.4429	-0.1930	-0.6426 - 0.3347

Table S4.2 Model selection. Where the correlations tested in Table S4.1 were significant, linear models were used to control for the effect of other environmental variables. The log likelihoods and degrees of freedom for all models tested are presented here.

Model	Log Likelihood (Max. Likelihood)	Degrees of freedom
log(Abundance)~ Disturbance rank	-16.6356	3
log(Abundance)~ Disturbance rank + Elevation	-16.2785	4
log(Abundance)~ Disturbance rank + Distance to river	-14.0386	5
log(Obs. Diversity q = 0) ~ Disturbance rank	-1.1849	3
log(Obs. Diversity q = 0) ~ Disturbance rank + Elevation	-1.0606	4
log(Obs. Diversity q = 0) ~ Disturbance rank + Distance to river	0.4615	4
log(Obs. Diversity q = 1) ~ Disturbance rank	-2.3260	3
log(Obs. Diversity q = 1) ~ Disturbance rank + Elevation	-2.1954	4
log(Obs. Diversity q = 1) ~ Disturbance rank + Distance to river	-1.3630	4
log(Obs. Diversity q = 2)~ Disturbance rank	-6.2357	3
log(Obs. Diversity q = 2) ~ Disturbance rank + Elevation	-5.9173	4
log(Obs. Diversity q = 2) ~ Disturbance rank + Distance to river	-5.6520	4
log(Obs. Diversity q = ∞) ~ Disturbance rank	-5.0875	3
log(Obs. Diversity q = ∞) ~ Disturbance rank + Elevation	-4.6954	4
log(Obs. Diversity q = ∞) ~ Disturbance rank + Distance to river	-4.8372	4
Vegetation structure PC1 ~ Disturbance rank	-6.4559	3
Vegetation structure PC1 ~ Disturbance rank + Elevation	-6.2303	4
Vegetation structure PC1 ~ Disturbance rank + Distance to river	-5.7609	4
log(Est. diversity q = 0) ~ Disturbance rank	6.70	3
log(Est. diversity q = 0) ~ Disturbance rank + Elevation	6.82	4
log(Est. diversity q = 0) ~ Disturbance rank + Distance to river	6.83	4
log(Est. diversity q = 1) ~ Disturbance rank	-2.15	3
log(Est. diversity q = 1) ~ Disturbance rank + Elevation	-1.86	4
log(Est. diversity q = 1) ~ Disturbance rank + Distance to river	-2.10	4
log(Est. diversity q = 2) ~ Disturbance rank	-5.87	3

Model	Log Likelihood (Max. Likelihood)	Degrees of freedom
log(Est. diversity q = 2) ~ Disturbance rank + Elevation	-5.50	4
log(Est. diversity q = 2) ~ Disturbance rank + Distance to river	-5.70	4
log(ρ Redundancy q = 1) ~ Disturbance rank	-13.3025	3
log(ρ Redundancy q = 1) ~ Disturbance rank + Elevation	-12.7122	4
log(ρ Redundancy q = 1) ~ Disturbance rank + Distance to river	-11.5194	4
log(ρ Representativeness q = 1) ~ Disturbance rank	6.1746	3
log(ρ Representativeness q = 1) ~ Disturbance rank + Elevation	6.1913	4
log(ρ Representativeness q = 1) ~ Disturbance rank + Distance to river	9.1013	4

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Table S4.3 Results of the best fitting models. The estimated coefficients and significance are presented for the explanatory variables found to produce the best fitting models identified in Table S4.2.

Model	Variable	Est. coefficient	SE	t	p
log(Abundance) ~ Disturbance rank + Distance to River	Rank	0.317	0.082	3.871	0.002
	Distance to river	-0.001	0.000	-2.240	0.041
log(Obs. Diversity q = 0) ~ Disturbance rank	Rank	0.103	0.038	2.724	0.015
log(Obs. Diversity q = 1) ~ Disturbance rank	Rank	0.077	0.040	1.914	0.074
log(Obs. Diversity q = 2) ~ Disturbance rank	Rank	0.087	0.050	1.730	0.103
log(Obs. Diversity q = ∞) ~ Disturbance rank	Rank	0.091	0.047	1.946	0.069
Vegetation structure PC1 ~ Disturbance rank	Rank	0.492	0.051	9.703	0.000
log(Est. diversity q = 0) ~ Disturbance rank	Rank	0.020	0.024	0.813	0.428
log(Est. diversity q = 1) ~ Disturbance rank	Rank	0.031	0.040	0.772	0.451
log(Est. diversity q = 2) ~ Disturbance rank	Rank	0.055	0.049	1.112	0.282
log(ρ Redundancy q = 1) ~ Disturbance rank	Rank	-0.217	0.074	-2.920	0.010
log(ρ Representativeness q = 1) ~ Disturbance rank + Distance to river	Rank	0.0711	0.0227	3.136	0.0068
	Distance to river	-0.0002	<0.0001	-2.401	0.0298

Table S4.4 Moran's I. Results of the tests for spatial autocorrelation performed on the residuals of the best fitting models (Table S4.3), for all models where a significant correlation was found.

Model	Observed	Expected	SD	p	Observed - Expected
log(Abundance) ~ Disturbance rank + Distance to river	-0.1074	-0.0588	0.0916	0.5950	-0.0487
log(Obs. Diversity q = 0) ~ Disturbance rank	-0.1237	-0.0588	0.0940	0.4901	-0.0649
log(Obs. Diversity q = 1) ~ Disturbance rank	-0.1346	-0.0588	0.0879	0.3883	-0.0757
log(Obs. Diversity q = 2) ~ Disturbance rank	-0.0950	-0.0588	0.0879	0.6806	-0.0362
log(Obs. Diversity q = ∞) ~ Disturbance rank	-0.0788	-0.0588	0.0912	0.8270	-0.0199
Vegetation structure PC1 ~ Disturbance rank	-0.0176	-0.0588	0.0958	0.6669	0.0412
log(Est. diversity q = 0) ~ Disturbance rank	-0.0403	-0.0588	0.0920	0.8401	0.0186
log(Est. diversity q = 1) ~ Disturbance rank	-0.0492	-0.0588	0.0889	0.9140	0.0096
log(Est. diversity q = 2) ~ Disturbance rank	-0.0648	-0.0588	0.0883	0.9464	-0.0059
log(ρ Redundancy q = 1) ~ Disturbance rank	0.00095	-0.0588	0.0914	0.5130	0.0598
log(ρ Representativeness q = 1) ~ Disturbance rank	-0.1439	-0.0588	0.0924	0.3570	-0.0851

Table S4.5 Species list of orchid bees found in study.

Species
Eufriesea magretti
Eufriesea pulchra
Eufriesea rufocauda
Euglossa allosticta
Euglossa augaspis
Euglossa bidentata
Euglossa chalybeata
Euglossa cognata
Euglossa crassipunctata
Euglossa despecta
Euglossa gaianii
Euglossa gorgonensis
Euglossa ignita
Euglossa imperialis
Euglossa intersecta
Euglossa ioprosopa
Euglossa laevicincta
Euglossa maculilabris
Euglossa mixta
Euglossa modestior
Euglossa occidentalis
Euglossa orellana
Euglossa perviridis
Euglossa viridifrons
Eulaema bombiformis
Eulaema cingulata
Eulaema meriana
Eulaema mocsaryi
Eulaema seabrai
Exaerete frontalis
Exaerete smaragdina

8.4 Chapter 5

8.4.1 Figures

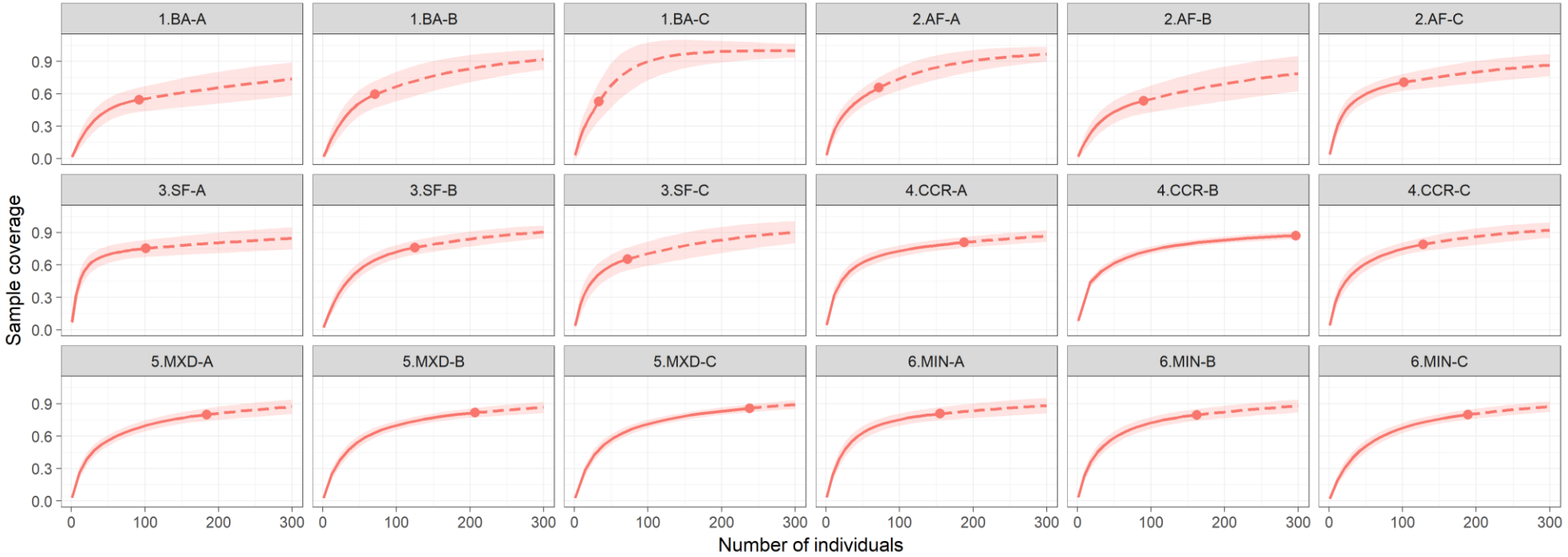
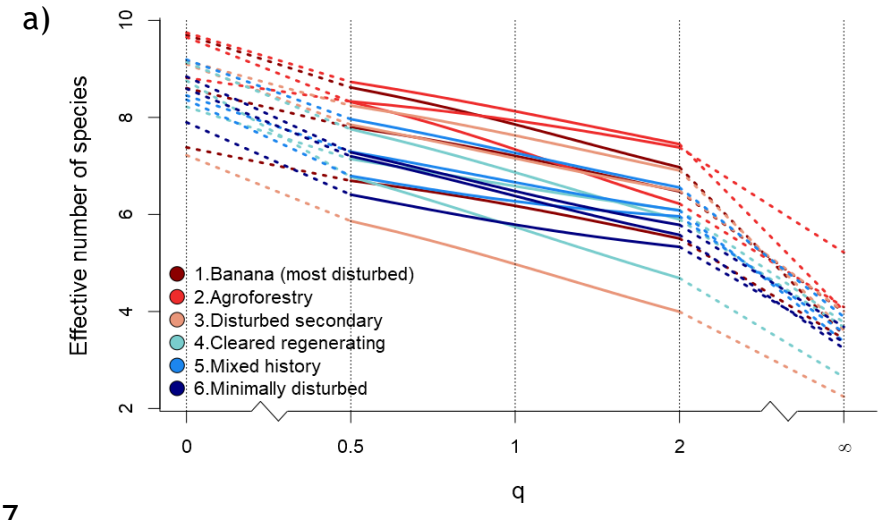


Figure S5.1 Sample completeness at each site. Numbers in the chart titles indicate the disturbance level of the site. Sample completeness is shown up until 300 individuals, the maximum sample size at an individual site. The solid red line represents the rarefied sample coverage and the dotted line show the extrapolated estimate, with a 95% confidence interval; the solid red circle indicates the collected sample size.



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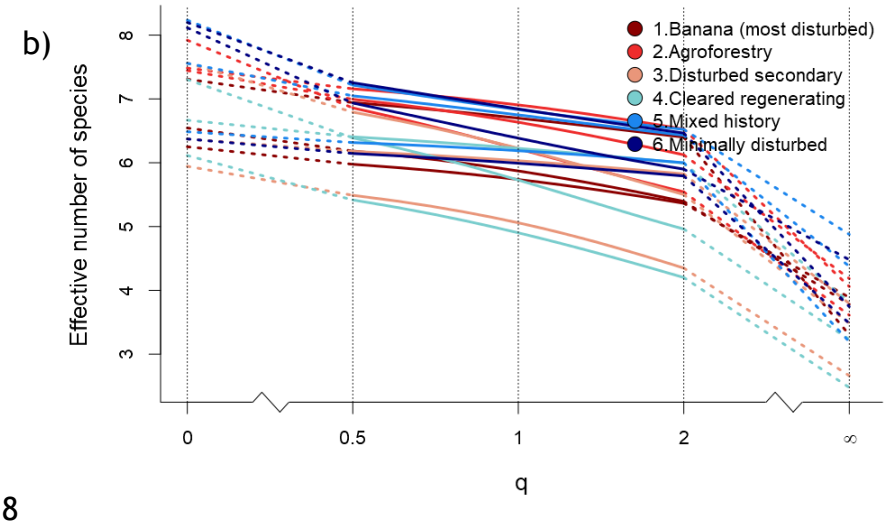

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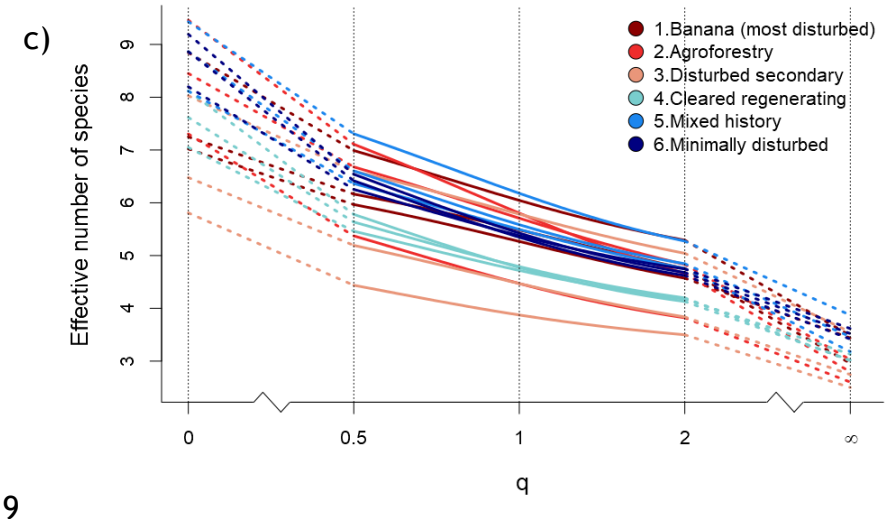
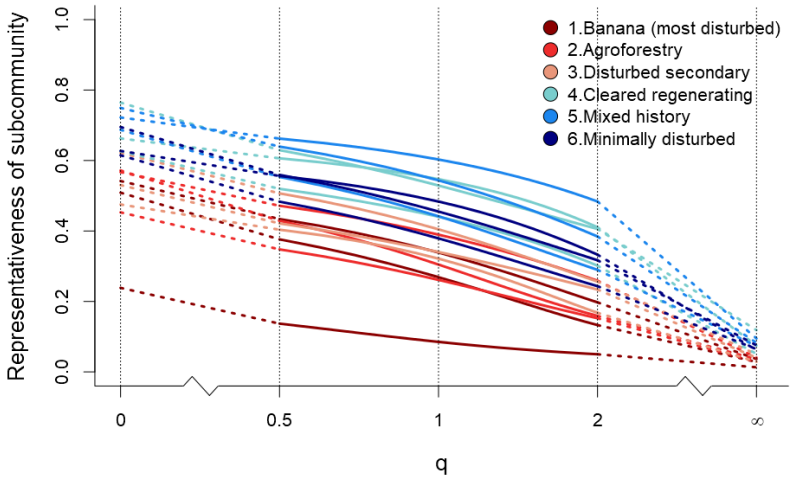


4219
4220 Figure S5.2 Similarity-sensitive alpha diversity across the disturbance gradient (a) for the original
4221 data collected during this study, (b) with the light-loving species removed, and (c) including high
4222 canopy trap data for the three least disturbed forest types (and the original data for the most disturbed
4223 categories).

a)



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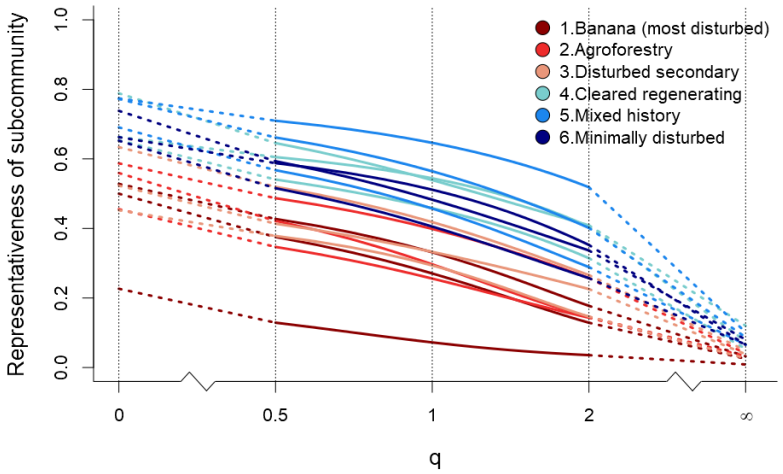
b)



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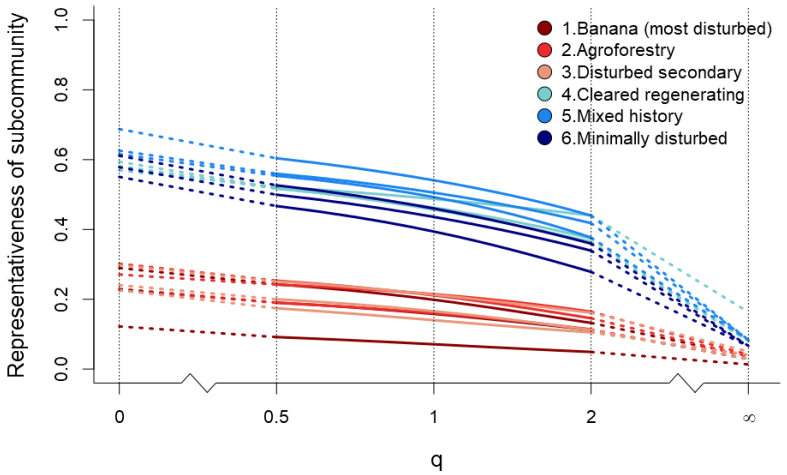
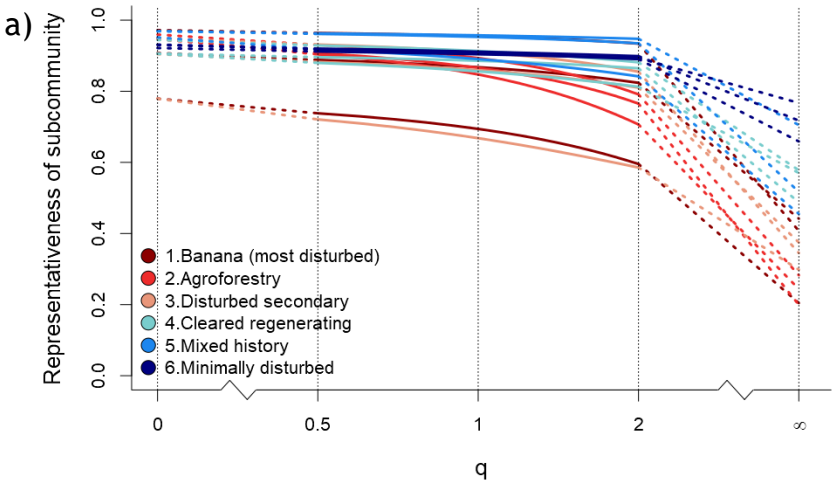
c)



4226
4227 Figure S5.3 Impact of light-loving species on naïve representativeness (a) of the original dataset, (b)
4228 removing the species known to favour well-lit open habitats from my dataset and (c) including high
4229 canopy data for ranks 4-6, to reflect what might have been found had I sampled all vertical strata.
4230 The disturbance ranking of the sites is indicated by a colour gradient going from dark red (most
4231 disturbed) to dark blue (least disturbed).



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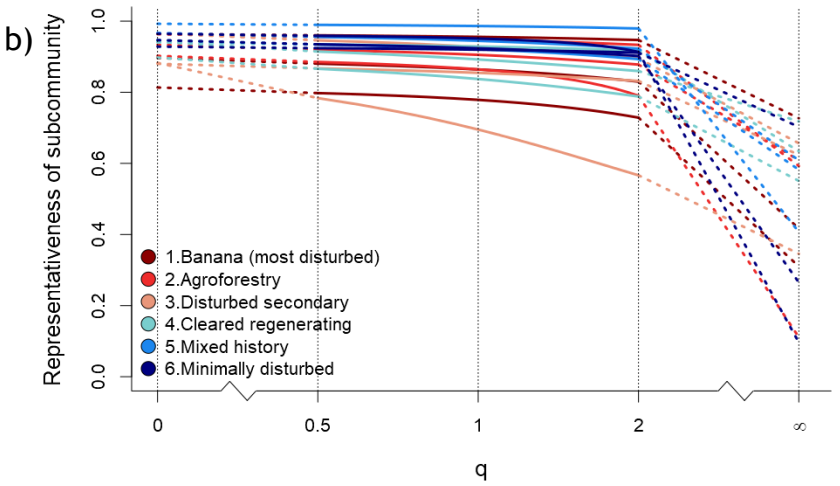

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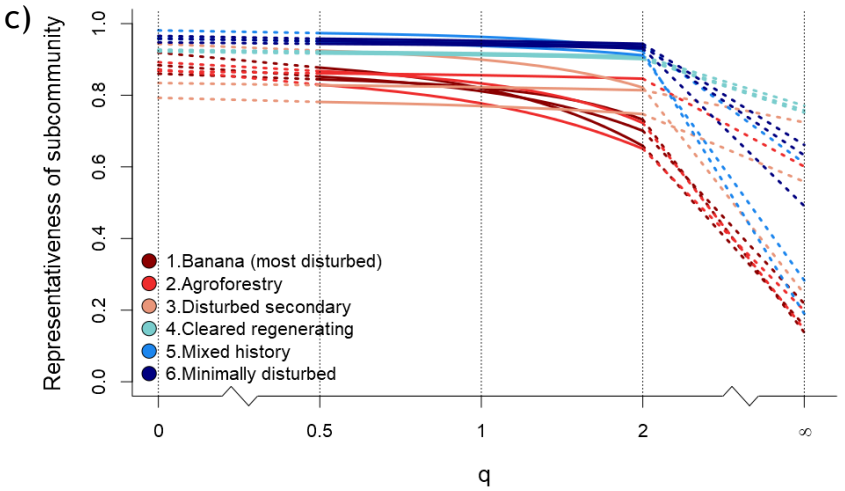
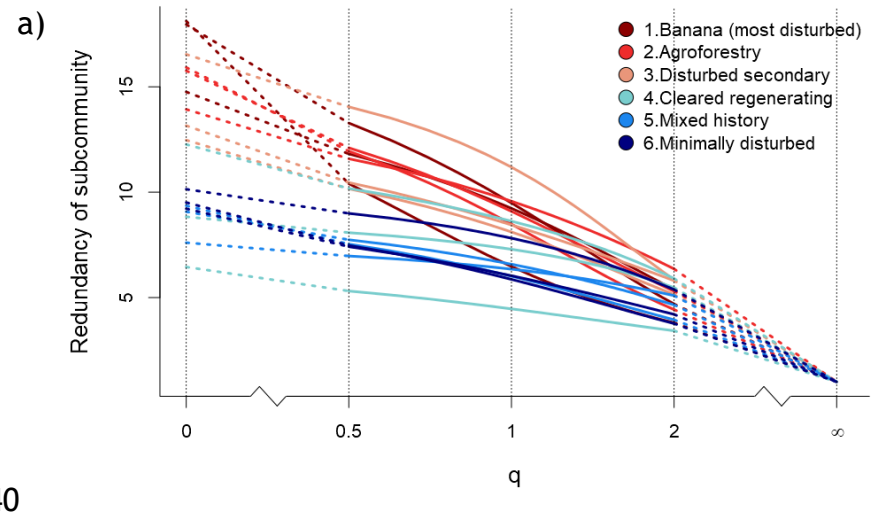


4234
4235 Figure S5.4 Similarity-sensitive representativeness of each site of the metacommunity (a) for the
4236 original data collected during this study, b) with the light-loving species removed, and c) including
4237 high canopy trap data for the three least disturbed forest types (and the original data for the most
4238 disturbed categories).

4239



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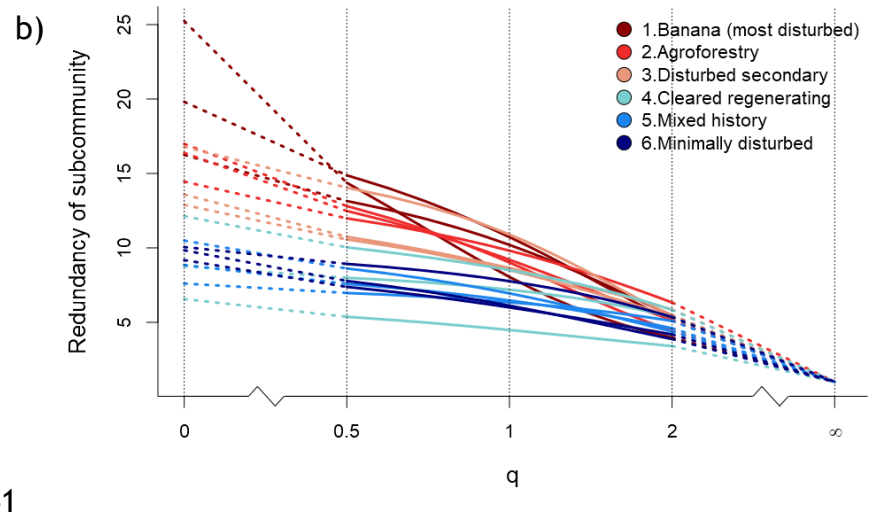

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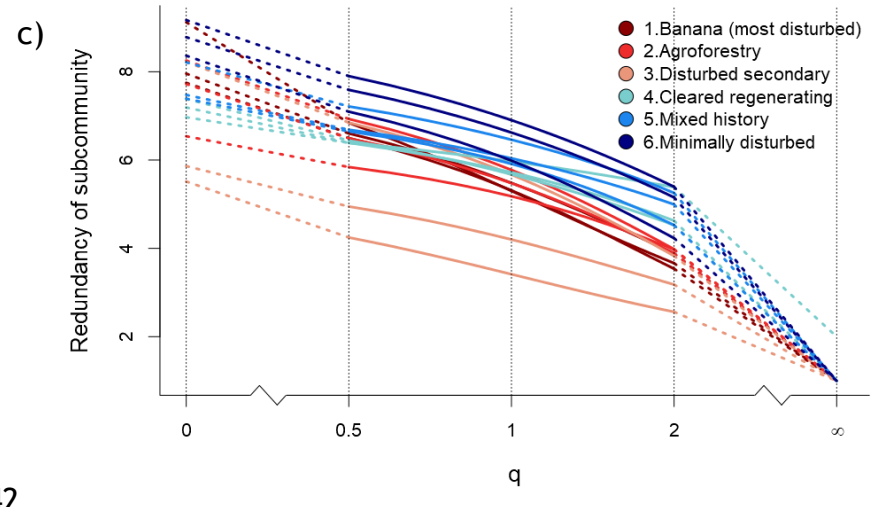
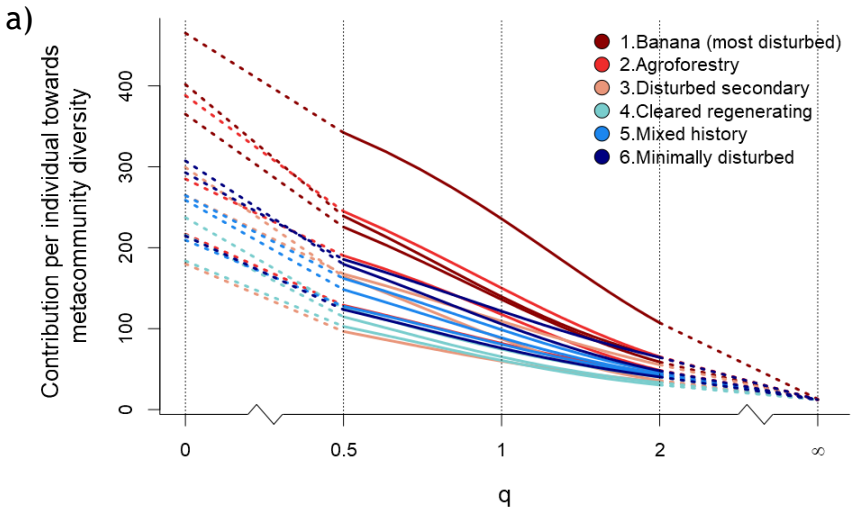
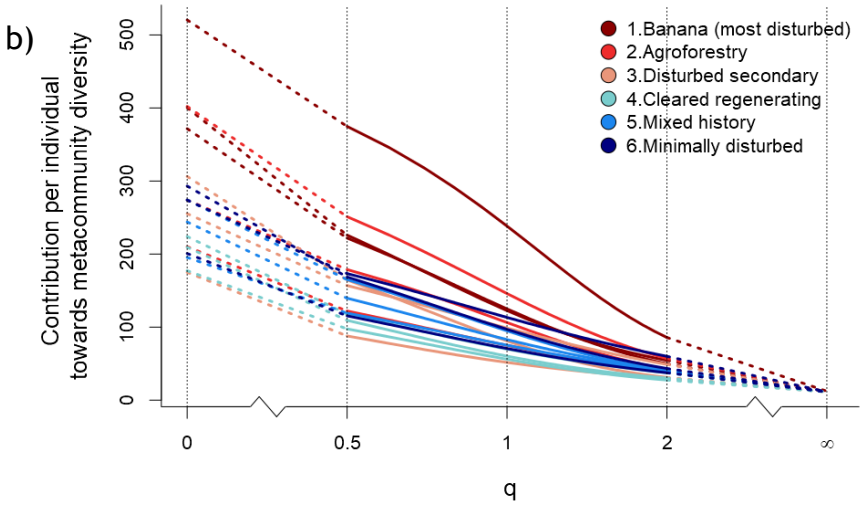


4242
4243 Figure S5.5 Naïve redundancy of the subcommunities across the disturbance gradient (a) with the
4244 original collected data, (b) with light-loving species removed and (c) including high canopy trap data
4245 for the three least disturbed forest types (and the original data for the most disturbed categories).

4246





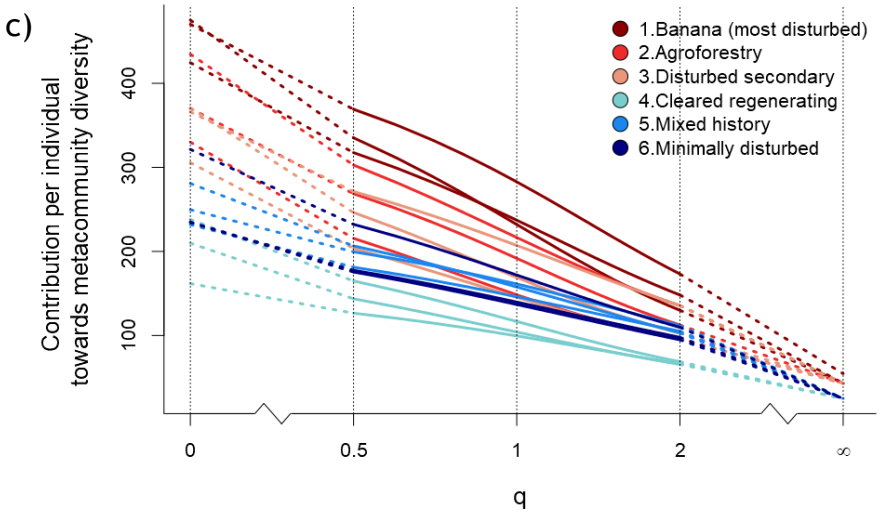


Figure S5.6 Naïve gamma diversity across the disturbance gradient. This represents the contribution of each site to the diversity of the overall metacommunity per individual detected (a) using original data collected during this study, (b) with the light-loving species removed, and (c) including high canopy trap data for the three least disturbed forest types (and the original data for the most disturbed categories).

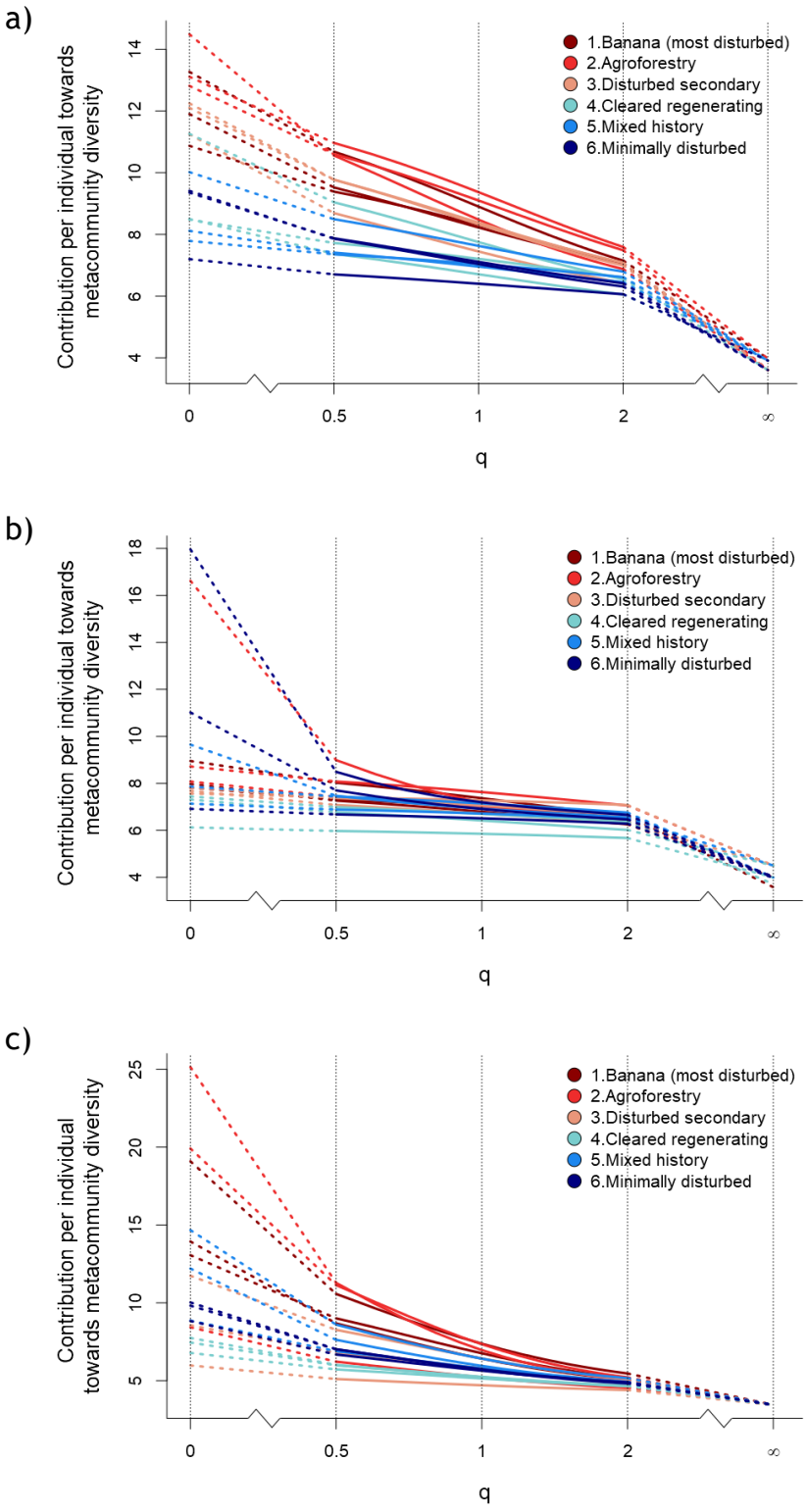


Figure S5.7 Similarity-sensitive subcommunity gamma diversity across the disturbance gradient. This is a measure of how much each site contributes to the overall diversity of the metacommunity per individual butterfly collected there (a) for the original data collected during this study, (b) with the light-loving species removed, and c) including high canopy trap for the three least disturbed forest types (and the original data for the most disturbed categories).

8.4.2 Tables

Table S5.1 Species list of butterflies found in the study, including their higher-level taxonomy. MSP stands for morphospecies number, and this is the number assigned to each butterfly new to our species list before it is identified to species level, if possible. Some specimens were simply defined as UID ('unidentified') if they were too old/worn or escaped before further identification was possible. Identification of all levels was not always possible, in which case 'n/a' was assigned to the missing information. The list has been sorted in alphabetical order starting from Family and moving down to species

MSP	Species	Genus	Tribe	Subfamily	Family
UID Hesperidae	*n/a*	n/a	n/a	n/a	Hesperidae
646	*Dyscophellus sp.646*	Dyscophellus	n/a	Eudaminae	Hesperiidae
505	*Euriphellus euribates*	Euriphellus	n/a	Eudaminae	Hesperiidae
680	*Saliana hewitsoni*	Saliana	Calpodini	Hesperiinae	Hesperiidae
677	*Saliana salius*	Saliana	Calpodini	Hesperiinae	Hesperiidae
581	*Saliana sp.581*	Saliana	Calpodini	Hesperiinae	Hesperiidae
532	*Perichares sp.532*	Perichares	Erionotini	Hesperiinae	Hesperiidae
702	*Hesperidae sp.702*	n/a	n/a	n/a	Hesperiidae
763	*Hesperiidae*	n/a	n/a	n/a	Hesperiidae
758	*Hesperiidae sp.*	n/a	n/a	n/a	Hesperiidae
774	*Hesperiidae sp.*	n/a	n/a	n/a	Hesperiidae
457	*Hesperiidae sp.457*	n/a	n/a	n/a	Hesperiidae
522	*Hesperiidae sp.522*	n/a	n/a	n/a	Hesperiidae
538	*Hesperiidae sp.538*	n/a	n/a	n/a	Hesperiidae
562	*Hesperiidae sp.562*	n/a	n/a	n/a	Hesperiidae
577	*Hesperiidae sp.577*	n/a	n/a	n/a	Hesperiidae
578	*Hesperiidae sp.578*	n/a	n/a	n/a	Hesperiidae
589	*Pythonides jovianus*	Pythonides	Achylodidini	Pyrginae	Hesperiidae
565	*Astraptes fuglerator*	Astraptes	Eudamini	Pyrginae	Hesperiidae
658	*Urbanus proteus*	Urbanus	Eudamini	Pyrginae	Hesperiidae
463	*Urbanus sp.463*	Urbanus	Eudamini	Pyrginae	Hesperiidae
596	*Jemadia sp.596*	Jemadia	Pyrrhopygini	Pyrrhopyginae	Hesperiidae

	MSP	Species	Genus	Tribe	Subfamily	Family
	451	*Pyrrhopyge phidias*	Pyrrhopyge	Pyrrhopygini	Pyrrhopyginae	Hesperiidae
UID Lycaenidae		*n/a*	n/a	n/a	n/a	Lycaenidae
	32	*Ostrinotes sp2*	Ostrinotes	Eumaeini	Theclinae	Lycaenidae
	718	*MSP 718*	n/a	n/a	n/a	n/a
	329	*n/a*	n/a	n/a	n/a	n/a
	785	*n/a*	n/a	n/a	n/a	n/a
	787	*n/a*	n/a	n/a	n/a	n/a
	830	*n/a*	n/a	n/a	n/a	n/a
	221	*UID4*	UID4	n/a	n/a	n/a
	254	*UID5*	UID5	n/a	n/a	n/a
	109	*Doxocopa agathina*	Doxocopa	Apaturinae	Apaturinae	Nymphalidae
	91	*Ectima iona*	Ectima	Ageroniini	Biblidinae	Nymphalidae
	181	*Ectima lirides*	Ectima	Ageroniini	Biblidinae	Nymphalidae
	160	*Hamadryas amphinome*	Hamadryas	Ageroniini	Biblidinae	Nymphalidae
	18	*Hamadryas chloe*	Hamadryas	Ageroniini	Biblidinae	Nymphalidae
	92	*Hamadryas iphthime iphthime*	Hamadryas	Ageroniini	Biblidinae	Nymphalidae
	143	*Hamydras laodamia*	Hamydras	Ageroniini	Biblidinae	Nymphalidae
	25	*Panacea prola*	Panacea	Ageroniini	Biblidinae	Nymphalidae
	96	*Panacea regina*	Panacea	Ageroniini	Biblidinae	Nymphalidae
	313	*Vila emilia*	Vila	Biblidini	Biblidinae	Nymphalidae
	262	*Diaethria clymena*	Diaethria	Callicorini	Biblidinae	Nymphalidae
	42	*Catonephele acontius*	Catonephele	Epicaliini	Biblidinae	Nymphalidae
	50	*Catonephele numilia*	Catonephele	Epicaliini	Biblidinae	Nymphalidae
	201	*Eunica orphise*	Eunica	Epicaliini	Biblidinae	Nymphalidae
	252	*Eunica pusilla*	Eunica	Epicaliini	Biblidinae	Nymphalidae
UID Eunica		*n/a*	Eunica	Epicaliini	Biblidinae	Nymphalidae
	138	*Epiphile lampethusa*	Epiphile	Epiphelini	Biblidinae	Nymphalidae

	MSP	Species	Genus	Tribe	Subfamily	Family
	170	*Pyrrhogyra crameri*	Pyrrhogyra	Epiphelini	Biblidinae	Nymphalidae
	71	*Pyrrhogyra otolais*	Pyrrhogyra	Epiphelini	Biblidinae	Nymphalidae
	61	*Temenis laothoe*	Temenis	Epiphelini	Biblidinae	Nymphalidae
	116	*Temenis pulchra*	Temenis	Epiphelini	Biblidinae	Nymphalidae
	389	*Nica flavilla*	Nica	Epiphilini	Biblidinae	Nymphalidae
	322	*Dynamine chryseis*	Dynamine	Eubagini	Biblidinae	Nymphalidae
	251	*Dynamine giselia*	Dynamine	Eubagini	Biblidinae	Nymphalidae
UID Biblidinae		*UID Biblidinae*	n/a	n/a	Biblidinae	Nymphalidae
	75	*Bia actorion*	Bia	Brassolini	Brassolinae	Nymphalidae
	208	*Caligo idomeneus*	Caligo	Brassolini	Brassolinae	Nymphalidae
	27	*Caligo euphorbus*	Caligo	Brassolini	Brassolinae	Nymphalidae
	95	*Caligo eurilochus*	Caligo	Brassolini	Brassolinae	Nymphalidae
	72	*Caligo illioneus*	Caligo	Brassolini	Brassolinae	Nymphalidae
	350	*Caligo sp.350*	Caligo	Brassolini	Brassolinae	Nymphalidae
	99	*Catoblepia berecynthia*	Catoblepia	Brassolini	Brassolinae	Nymphalidae
	98	*Catoblepia xanthicles*	Catoblepia	Brassolini	Brassolinae	Nymphalidae
	142	*Narope cyllabarus*	Narope	Brassolini	Brassolinae	Nymphalidae
	380	*Narope nesope*	Narope	Brassolini	Brassolinae	Nymphalidae
	511	*Narope sp.511*	Narope	Brassolini	Brassolinae	Nymphalidae
	540	*Narope sp.540*	Narope	Brassolini	Brassolinae	Nymphalidae
	89	*Narope sp.89*	Narope	Brassolini	Brassolinae	Nymphalidae
	379	*Narope syllabus*	Narope	Brassolini	Brassolinae	Nymphalidae
	387	*Opoptera aorsa*	Opoptera	Brassolini	Brassolinae	Nymphalidae
	90	*Opsiphanes cassina*	Opsiphanes	Brassolini	Brassolinae	Nymphalidae
	123	*Opsiphanes invirae*	Opsiphanes	Brassolini	Brassolinae	Nymphalidae
	440	*Selenophanes cassiope*	Selenophanes	Brassolini	Brassolinae	Nymphalidae
	84	*Consul fabius*	Consul	Anaeini	Charaxinae	Nymphalidae

	MSP	Species	Genus	Tribe	Subfamily	Family
	67	*Fountainea eurypyle*	Fountainea	Anaeini	Charaxinae	Nymphalidae
	83	*Fountainea ryphea*	Fountainea	Anaeini	Charaxinae	Nymphalidae
	701	*Fountainea sp.701*	Fountainea	Anaeini	Charaxinae	Nymphalidae
	57	*Hypna clytemnestra negra*	Hypna	Anaeini	Charaxinae	Nymphalidae
	157	*Memphis acaudata*	Memphis	Anaeini	Charaxinae	Nymphalidae
	224	*Memphis acidalia*	Memphis	Anaeini	Charaxinae	Nymphalidae
	108	*Memphis basilia*	Memphis	Anaeini	Charaxinae	Nymphalidae
	366	*Memphis basilia*	Memphis	Anaeini	Charaxinae	Nymphalidae
	22	*Memphis glauce*	Memphis	Anaeini	Charaxinae	Nymphalidae
	433	*Memphis moruus*	Memphis	Anaeini	Charaxinae	Nymphalidae
	24	*Memphis offa*	Memphis	Anaeini	Charaxinae	Nymphalidae
	21	*Memphis phantes*	Memphis	Anaeini	Charaxinae	Nymphalidae
	110	*Memphis philomena*	Memphis	Anaeini	Charaxinae	Nymphalidae
	275	*Memphis pithyusa*	Memphis	Anaeini	Charaxinae	Nymphalidae
	97	*Memphis praxias*	Memphis	Anaeini	Charaxinae	Nymphalidae
	482	*Memphis pseudiphis*	Memphis	Anaeini	Charaxinae	Nymphalidae
	737	*Memphis sp.*	Memphis	Anaeini	Charaxinae	Nymphalidae
	190	*Memphis sp.190*	Memphis	Anaeini	Charaxinae	Nymphalidae
	402	*Memphis sp.402*	Memphis	Anaeini	Charaxinae	Nymphalidae
	444	*Memphis sp.444*	Memphis	Anaeini	Charaxinae	Nymphalidae
	445	*Memphis sp.445*	Memphis	Anaeini	Charaxinae	Nymphalidae
	592	*Memphis sp.592*	Memphis	Anaeini	Charaxinae	Nymphalidae
	34	*Memphis sp3*	Memphis	Anaeini	Charaxinae	Nymphalidae
	20	*Memphis sp7*	Memphis	Anaeini	Charaxinae	Nymphalidae
	223	*Memphis xenocles*	Memphis	Anaeini	Charaxinae	Nymphalidae
UID Memphis		*n/a*	Memphis	Anaeini	Charaxinae	Nymphalidae
	88	*Zaretis itys*	Zaretis	Anaeini	Charaxinae	Nymphalidae

	MSP	Species	Genus	Tribe	Subfamily	Family
	31	*Archaeoprepona demophon*	Archaeoprepona	Preponini	Charaxinae	Nymphalidae
	186	*Archaeoprepona demophoon*	Archaeoprepona	Preponini	Charaxinae	Nymphalidae
	624	*Archaeoprepona licomedes*	Archaeoprepona	Preponini	Charaxinae	Nymphalidae
	327	*Archaeoprepona meander*	Archaeoprepona	Preponini	Charaxinae	Nymphalidae
	266	*Prepona amydon*	Prepona	Preponini	Charaxinae	Nymphalidae
	127	*Prepona claudina*	Prepona	Preponini	Charaxinae	Nymphalidae
	187	*Prepona dexamenus*	Prepona	Preponini	Charaxinae	Nymphalidae
	130	*Prepona laertes*	Prepona	Preponini	Charaxinae	Nymphalidae
	375	*Prepona sp.375*	Prepona	Preponini	Charaxinae	Nymphalidae
	441	*Prepona sp.441*	Prepona	Preponini	Charaxinae	Nymphalidae
	230	*Lycorea halia*	Lycorea	Danaini	Danainae	Nymphalidae
	203	*Ceratina sp1*	Ceratina	Ithomiini	Danainae	Nymphalidae
	36	*Hypoleria lavinia*	Hypoleria	Ithomiini	Danainae	Nymphalidae
	243	*Hyposcada anchiala anchiata*	Hyposcada	Ithomiini	Danainae	Nymphalidae
	103	*Hypothyris ninonia*	Hypothyris	Ithomiini	Danainae	Nymphalidae
	70	*Napeogenes juanjuiensis*	Napeogenes	Ithomiini	Danainae	Nymphalidae
	234	*Oleria sp.234*	Oleria	Ithomiini	Danainae	Nymphalidae
	205	*Oleria victorine*	Oleria	Ithomiini	Danainae	Nymphalidae
	209	*Rhodussa cantobrica*	Rhodussa	Ithomiini	Danainae	Nymphalidae
	46	*Tithorea harmonia*	Tithorea	Ithomiini	Danainae	Nymphalidae
	537	*Tithorea sp.537*	Tithorea	Ithomiini	Danainae	Nymphalidae
	684	*Danainae sp.684*	n/a	n/a	Danainae	Nymphalidae
UID Ithomine		*n/a*	n/a	n/a	Danainae	Nymphalidae
UID Heliconiae		*n/a*	n/a	n/a	Heliconiae	Nymphalidae
	105	*Heliconius burneyi*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	29	*Heliconius doris*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	207	*Heliconius emma*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae

	MSP	Species	Genus	Tribe	Subfamily	Family
	194	*Heliconius erato*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	40	*Heliconius hecale*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	183	*Heliconius leucadia*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	175	*Heliconius melpomeme*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	43	*Heliconius melpomene*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	39	*Heliconius numata*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	572	*Heliconius numata arcuella?*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	45	*Heliconius pardalinus*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	28	*Heliconius sara*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	403	*Heliconius sp.403*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	424	*Heliconius sp.424*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	551	*Heliconius sp.551*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	344	*Heliconius wallacei*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	177	*Heliconius xanthocles*	Heliconius	Heliconiini	Heliconiinae	Nymphalidae
	44	*Neruda aoede*	Neruda	Heliconiini	Heliconiinae	Nymphalidae
	55	*Philaethria dido*	Philaethria	Heliconiini	Heliconiinae	Nymphalidae
	299	*Adelpha delinita*	Adelpha	Limeniditini	Limenitidinae	Nymphalidae
	750	*Adelpha messara*	Adelpha	Limeniditini	Limenitidinae	Nymphalidae
	710	*Adelpha sp.710*	Adelpha	Limeniditini	Limenitidinae	Nymphalidae
	364	*Adelpha thesprotia*	Adelpha	Limeniditini	Limenitidinae	Nymphalidae
UID Adelpha		*n/a*	Adelpha	Limeniditini	Limenitidinae	Nymphalidae
	342	*Adelpha attica*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	176	*Adelpha boeotia*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	214	*Adelpha capucinus*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	54	*Adelpha cocala*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	231	*Adelpha cytherea*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	315	*Adelpha erotia*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae

	MSP	Species	Genus	Tribe	Subfamily	Family
	120	*Adelpha iphiclus*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	182	*Adelpha jordani*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	264	*Adelpha melona*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	128	*Adelpha mesentina*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	232	*Adelpha pleasure*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	56	*Adelpha zina*	Adelpha	Limenitidini	Limenitidinae	Nymphalidae
	621	*Antirrhea hela*	Antirrhea	Morphini	Morphinae	Nymphalidae
	104	*Morpho helenor*	Morpho	Morphini	Morphinae	Nymphalidae
	26	*Morpho achilles*	Morpho	Morphini	Morphinae	Nymphalidae
	786	*Morpho sp.*	Morpho	Morphini	Morphinae	Nymphalidae
UID Morpho		*n/a*	Morpho	Morphini	Morphinae	Nymphalidae
	33	*Nessaea hewitsonii*	Nessaea	Catonephelini	n/a	Nymphalidae
	49	*Nessaea obrinus*	Nessaea	Catonephelini	n/a	Nymphalidae
	53	*Baeotus aeilus*	Baeotus	Coeini	Nymphalinae	Nymphalidae
	216	*Baeotus beotus*	Baeotus	Coeini	Nymphalinae	Nymphalidae
UID Baeotus		*n/a*	Baeotus	Coeini	Nymphalinae	Nymphalidae
	167	*Historis acheronta*	Historis	Coeini	Nymphalinae	Nymphalidae
	119	*Historis odius*	Historis	Coeini	Nymphalinae	Nymphalidae
	135	*Manataria hercyna*	Manataria	Melitaeini	Nymphalinae	Nymphalidae
	343	*Manataria hercyna*	Manataria	Melitaeini	Nymphalinae	Nymphalidae
	472	*Telenassa jana*	Telenassa	Melitaeini	Nymphalinae	Nymphalidae
	627	*Colobura annulata*	Colobura	Nymphalini	Nymphalinae	Nymphalidae
	58	*Colobura dirce*	Colobura	Nymphalini	Nymphalinae	Nymphalidae
	179	*Siproeta stelenes*	Siproeta	Nymphalini	Nymphalinae	Nymphalidae
	132	*Smyrna blomfildia*	Smyrna	Nymphalini	Nymphalinae	Nymphalidae
	51	*Tigridia acesta*	Tigridia	Nymphalini	Nymphalinae	Nymphalidae
	274	*Metamorpha elissa*	Metamorpha	Victorinini	Nymphalinae	Nymphalidae

MSP	Species	Genus	Tribe	Subfamily	Family
428	*Chloreuptychia sp.428*	Chloreuptychia	Euptychiini	Satyrinae	Nymphalidae
UID Chloreuptychia	*n/a*	Chloreuptychia	Euptychiini	Satyrinae	Nymphalidae
271	*Euptychoides saturnus*	Euptychoides	Euptychiini	Satyrinae	Nymphalidae
669	*Pareuptychia summandosa*	Pareuptychia	Euptychiini	Satyrinae	Nymphalidae
14	*Splendeuptychia ashna*	Splendeuptychia	Euptychiini	Satyrinae	Nymphalidae
242	*Splendeuptychia aurigera*	Splendeuptychia	Euptychiini	Satyrinae	Nymphalidae
367	*Splendeuptychia kendalli*	Splendeuptychia	Euptychiini	Satyrinae	Nymphalidae
165	*Haetera piera*	Haetera	Haeterini	Satyrinae	Nymphalidae
UID Satyrinae	*n/a*	n/a	n/a	Satyrinae	Nymphalidae
704	*Satyrinae sp.704*	n/a	n/a	Satyrinae	Nymphalidae
1	*Parypthimoides undulate*	Parypthimoides	n/a	Satyrinae	Nymphalidae
219	*Amphidecta pignerator*	Amphidecta	Satyrini	Satyrinae	Nymphalidae
115	*Caeruleuptychia cyanites*	Caeruleuptychia	Satyrini	Satyrinae	Nymphalidae
30	*Caeruleuptychia ziza*	Caeruleuptychia	Satyrini	Satyrinae	Nymphalidae
278	*Cepheuptychia glaucina*	Cepheuptychia	Satyrini	Satyrinae	Nymphalidae
198	*Chloreuptychia agatha*	Chloreuptychia	Satyrini	Satyrinae	Nymphalidae
151	*Chloreuptychia arnaca*	Chloreuptychia	Satyrini	Satyrinae	Nymphalidae
122	*Chloreuptychia chlorimene*	Chloreuptychia	Satyrini	Satyrinae	Nymphalidae
114	*Chloreuptychia herseis*	Chloreuptychia	Satyrini	Satyrinae	Nymphalidae
69	*Cissia proba*	Cissia	Satyrini	Satyrinae	Nymphalidae
93	*Cissia sp1*	Cissia	Satyrini	Satyrinae	Nymphalidae
13	*Cissia terrestris*	Cissia	Satyrini	Satyrinae	Nymphalidae
12	*Erichthodes antonina*	Erichthodes	Satyrini	Satyrinae	Nymphalidae
9	*Harjesia blanda*	Harjesia	Satyrini	Satyrinae	Nymphalidae
8	*Harjesia obscura*	Harjesia	Satyrini	Satyrinae	Nymphalidae
270	*Hermeuptychia fallax*	Hermeuptychia	Satyrini	Satyrinae	Nymphalidae

	MSP	Species	Genus	Tribe	Subfamily	Family
	700	*Hermeuptychia sp.700*	Hermeuptychia	Satyrini	Satyrinae	Nymphalidae
	393	*Hermeuptychia sp.393*	Hermeuptychia	Satyrini	Satyrinae	Nymphalidae
	392	*Magneuptychia lybie*	Magneuptychia	Satyrini	Satyrinae	Nymphalidae
	7	*Magneuptychia modesta*	Magneuptychia	Satyrini	Satyrinae	Nymphalidae
	550	*Megeuptychia antonoe*	Megeuptychia	Satyrini	Satyrinae	Nymphalidae
	129	*Satyrinae sp1*	n/a	Satyrini	Satyrinae	Nymphalidae
	63	*Pareuptychia ocirrhoe*	Pareuptychia	Satyrini	Satyrinae	Nymphalidae
	154	*Posttaygetis penelea*	Posttaygetis	Satyrini	Satyrinae	Nymphalidae
	681	*Pseudodebis marpessa*	Pseudodebis	Satyrini	Satyrinae	Nymphalidae
	5	*Pseudodebis valentina*	Pseudodebis	Satyrini	Satyrinae	Nymphalidae
	244	*Rareuptychia clio*	Rareuptychia	Satyrini	Satyrinae	Nymphalidae
	11	*Taygetamorpha celia*	Taygetamorpha	Satyrini	Satyrinae	Nymphalidae
	663	*Taygetis cleopatra*	Taygetis	Satyrini	Satyrinae	Nymphalidae
	166	*Taygetis inambari*	Taygetis	Satyrini	Satyrinae	Nymphalidae
	6	*Taygetis larua*	Taygetis	Satyrini	Satyrinae	Nymphalidae
	10	*Taygetis mermeria*	Taygetis	Satyrini	Satyrinae	Nymphalidae
	638	*Taygetis sp.638*	Taygetis	Satyrini	Satyrinae	Nymphalidae
	62	*Taygetis sylvia*	Taygetis	Satyrini	Satyrinae	Nymphalidae
	237	*Taygetis thamyra*	Taygetis	Satyrini	Satyrinae	Nymphalidae
	82	*Taygetis virgilia*	Taygetis	Satyrini	Satyrinae	Nymphalidae
UID Taygetis		*UID Taygetis*	Taygetis	Satyrini	Satyrinae	Nymphalidae
	2	*Yphthimoides renata*	Yphthimoides	Satyrini	Satyrinae	Nymphalidae
	111	*Myscelia capenas*	Myscelia	Catonephelini		Nymphalidae
	459	*Pieridae sp.459*	n/a	n/a	n/a	Pieridae
	287	*Anteos menippe*	Anteos	n/a	Pierinae	Pieridae
	371	*Perrhybris pamela*	Perrhybris	Pierini	Pierinae	Pieridae
	760	*Riodinidae sp. 9*	n/a	n/a	n/a	Riodinidae

MSP	Species	Genus	Tribe	Subfamily	Family
384	*Riodinidae sp.384*	n/a	n/a	n/a	Riodinidae
241	*Eurybia elvina*	Eurybia	Eurybiini	Riodininae	Riodinidae
334	*Eurybia halimede*	Eurybia	Eurybiini	Riodininae	Riodinidae
3	*Eurybia unxia*	Eurybia	Eurybiini	Riodininae	Riodinidae
369	*Anteros kupris*	Anteros	Helicopini	Riodininae	Riodinidae
687	*Anteros sp. 687*	Anteros	Helicopini	Riodininae	Riodinidae
648	*Emesis lucinda*	Emesis	Helicopini	Riodininae	Riodinidae
407	*Emesis sp.407*	Emesis	Helicopini	Riodininae	Riodinidae
560	*Emesis sp.560*	Emesis	Helicopini	Riodininae	Riodinidae
159	*Emesis sp2*	Emesis	Helicopini	Riodininae	Riodinidae
475	*Sarota sp. 475*	Sarota	Helicopini	Riodininae	Riodinidae
470	*Sarota sp.470*	Sarota	Helicopini	Riodininae	Riodinidae
557	*Detritivora caryatis*	Detritivora	n/a	Riodininae	Riodinidae
280	*Adelotypa violacea*	Adelotypa	Nymphidiini	Riodininae	Riodinidae
220	*Thisbe irenea*	Thisbe	Nymphidini	Riodininae	Riodinidae
272	*Ancyluris meliboeus*	Ancyluris	Riodinini	Riodininae	Riodinidae
76	*Ancylurius meneria*	Ancylurius	Riodinini	Riodininae	Riodinidae
514	*Echydna punctata*	Echydna	Riodinini	Riodininae	Riodinidae
449	*Lyropteryx apollonia*	Lyropteryx	Riodinini	Riodininae	Riodinidae
276	*Rhetus periander*	Rhetus	Riodinini	Riodininae	Riodinidae

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4273 Table S5.2 Results of the Spearman rank correlation tests. The p-value and correlation coefficient, rho, along with a 95% confidence interval of the correlation, are
4274 shown for the results of correlation tests between each pair of variables 1 and 2.

Variable 1	Variable 2	p	Rho	Rho lower 95% Confidence	Rho upper 95% Confidence
Naïve Alpha q0	Rank	0.004642	0.634919	0.2810996	0.836402
Naïve Alpha q1	Rank	0.095986	0.404421	-0.1010448	0.7913462
Naïve Alpha q2	Rank	0.701249	0.097186	-0.4255457	0.590237
Naïve Alpha qInf	Rank	0.862639	-0.04391	-0.5064925	0.49655187
Similarity-sensitive Alpha q0	Rank	0.28512	-0.26648	-0.7153662	0.2242979
Similarity-sensitive Alpha q1	Rank	0.043973	-0.47966	-0.8241165	-0.0244271
Similarity-sensitive Alpha q2	Rank	0.058056	-0.45458	-0.8090935	-0.007438026
Similarity-sensitive Alpha qInf	Rank	0.120529	-0.37934	-0.7346693	0.09106909
Naïve Gamma q0	Rank	0.050645	-0.46712	-0.818098	0.1057877
Naïve Gamma q1	Rank	0.062052	-0.44831	-0.7866265	0.1235031
Naïve Gamma q2	Rank	0.090462	-0.41069	-0.7706352	0.1604621
Similarity-sensitive Gamma q0	Rank	0.000197	-0.76809	-0.910981	-0.5061388
Similarity-sensitive Gamma q1	Rank	6.87E-05	-0.79944	-0.9090014	-0.5568915
Similarity-sensitive Gamma q2	Rank	0.000132	-0.78063	-0.9065795	-0.5218936
Estimated Alpha q0	Rank	0.950775	-0.01568	-0.5618839	0.5784686
Estimated Alpha q1	Rank	0.462468	-0.18497	-0.6390272	0.3716097
Estimated Alpha q2	Rank	0.28512	-0.26648	-0.690561	0.2851713
Estimated Alpha q0 Proportion higher in good habitat (1000 runs)	Difference between ranks	0.834509	-0.05902	-0.5314514	0.4408466
Estimated Alpha q1 Proportion higher in good habitat (1000 runs)	Difference between ranks	0.493462	-0.1918	-0.653957	0.2987416
Estimated Alpha q2 Proportion higher in good habitat (1000 runs)	Difference between ranks	0.714156	-0.10328	-0.5564705	0.3575353
Naïve Rho q0	Rank	0.000107	-0.7869	-0.9198639	-0.4506966
Naïve Rho q1	Rank	0.002792	-0.66149	-0.8828746	-0.2901997
Naïve Rho q2	Rank	0.388607	-0.21632	-0.6343759	0.2810413

Variable 1	Variable 2	p	Rho	Rho lower 95% Confidence	Rho upper 95% Confidence
Similarity-sensitive Redundancy q0	Rank	4.27E-05	-0.81198	-0.9311359	-0.50679
Similarity-sensitive Redundancy q1	Rank	4.27E-05	-0.81198	-0.9314823	-0.5056606
Similarity-sensitive Redundancy q2	Rank	6.87E-05	-0.79944	-0.9324091	-0.4634454
Similarity-sensitive Redundancy qInf	Rank	0.454543	-0.1882	-0.6562064	0.3852609
Naïve Representativeness q0	Rank	0.000345	0.749275	0.4521353	0.8900594
Naïve Representativeness q1	Rank	0.000345	0.749275	0.409278	0.9111224
Naïve Representativeness q2	Rank	0.000488	0.736735	0.3667061	0.901988
Naïve Representativeness qInf	Rank	6.02E-05	0.802985	0.4967297	0.92039448
Similarity-sensitive Representativeness q0	Rank	0.833644	0.053296	-0.4712071	0.5394575
Similarity-sensitive Representativeness q1	Rank	0.080111	0.423231	-0.07539199	0.753639
Similarity-sensitive Representativeness q2	Rank	0.009565	0.592523	0.1209675	0.889466
Similarity-sensitive Representativeness qInf	Rank	1.96E-05	0.830786	0.5585528	0.95147083
Combined canopy Naïve Alpha q1	Rank	8.6E-05	0.793166	0.4916031	0.91185
Combined canopy Naïve Redundancy q1	Rank	6.87E-05	0.799436	0.4562114	0.9318214
Combined canopy Naïve Representativeness q1	Rank	0.000345	0.749275	0.4464298	0.8878858
Combined canopy Naïve Gamma q1	Rank	0.004021	-0.64268	-0.8878292	-0.1753832
Combined canopy Similarity-sensitive Alpha q1	Rank	0.891944	-0.03449	-0.4817159	0.4441766
Combined canopy Similarity-sensitive Redundancy q1	Rank	0.000488	-0.73674	-0.8942949	-0.3427753
Combined canopy Similarity-sensitive Representativeness q1	Rank	2.97E-06	0.868407	0.6379925	0.959101
Combined canopy Similarity-sensitive Gamma q1	Rank	0.062052	-0.44831	-0.763182	0.07459596
Light species excluded Naïve Alpha q1	Rank	0.040899	0.485932	0.01951195	0.8066711
Light species excluded Naïve Redundancy q1	Rank	0.000132	-0.78063	-0.9409945	-0.5135709
Light species excluded Naïve Representativeness q1	Rank	0.000197	0.768086	0.4564223	0.8972664
Light species excluded Naïve Gamma q1	Rank	0.075274	-0.4295	-0.777569	0.1533055
Light species excluded Similarity-sensitive Alpha q1	Rank	0.526249	0.159887	-0.3528716	0.6154758

Variable 1	Variable 2	p	Rho	Rho lower 95% Confidence	Rho upper 95% Confidence
Light species excluded Similarity-sensitive Redundancy q1	Rank	2.57E-05	-0.82452	-0.9394732	-0.5412245
Light species excluded Similarity-sensitive Representativeness q1	Rank	0.182248	0.32918	-0.187642	0.7319259
Light species excluded Similarity-sensitive Gamma q1	Rank	0.149199	-0.35426	-0.7030582	0.1210051
Abundance of butterflies at each site	Rank	6.0231e-05	0.8029	0.4942568	0.9207064

Table S5.3 Model selection including environmental variables. Linear models were used to control for the effect of other environmental variables in the data, namely the distance of the site to the river, and the elevation of the site.

Response	Explanatory variables	Log Likelihood	Degrees of freedom
Naïve Alpha q0	Rank	0.580956	3
Naïve Alpha q0	Rank + Elevation	1.620808	4
Naïve Alpha q0	Rank + Distance to river	1.254323	4
Naive Alpha q1	Rank	-0.4948416	3
Naive Alpha q1	Rank + Elevation	1.8469303	4
Naive Alpha q1	Rank + Distance to river	0.8877056	4
Naive Gamma q1	Rank	-3.957137	3
Naive Gamma q1	Rank + Elevation	-2.704240	4
Naive Gamma q1	Rank + Distance to river	-3.679884	4
Naïve Redundancy q1	Rank	4.885064	3
Naïve Redundancy q1	Rank + Elevation	5.188658	4
Naïve Redundancy q1	Rank + Distance to river	4.88553	4
Naïve Representativeness q1	Rank	-5.007078	3
Naïve Representativeness q1	Rank + Elevation	-4.997597	4
Naïve Representativeness q1	Rank + Distance to river	-4.855143	4
Similarity-sensitive Alpha q0	Rank	19.5405	3
Similarity-sensitive Alpha q0	Rank + Elevation	19.96976	4
Similarity-sensitive Alpha q0	Rank + Distance to river	19.97748	4
Similarity-sensitive Alpha q1	Rank	13.70962	3

Response	Explanatory variables	Log Likelihood	Degrees of freedom
Similarity-sensitive Alpha q1	Rank + Elevation	14.53267	4
Similarity-sensitive Alpha q1	Rank + Distance to river	14.21089	4
Similarity-sensitive Gamma q1	Rank	24.94245	3
Similarity-sensitive Gamma q1	Rank + Elevation	25.0357	4
Similarity-sensitive Gamma q1	Rank + Distance to river	24.95168	4
Similarity-sensitive Redundancy q1	Rank	-3.740062	3
Similarity-sensitive Redundancy q1	Rank + Elevation	-3.711686	4
Similarity-sensitive Redundancy q1	Rank + Distance to river	-3.718882	4
Similarity-sensitive Representativeness q1	Rank	18.4621	3
Similarity-sensitive Representativeness q1	Rank + Elevation	19.39706	4
Similarity-sensitive Representativeness q1	Rank + Distance to river	19.4695	4

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Table S5.4 Results of the best fitting linear models. The estimated coefficients and significance are presented for the explanatory variables found to produce the best fitting models identified in Table S5.3. The latter part of the table contains the linear models including spatial coordinates to account for possible spatial autocorrelation indicated by the results of the Moran's I test.

Response	Explanatory Variable	Estimated coefficient	SE Est. Coeff.	p
Naïve Alpha q0	Rank	0.122	0.0343	0.0139
Naive Alpha q1	Rank	0.06797	0.03641	0.00254
Naive Gamma q1	Rank	-0.09916	0.04413	0.0391
Naïve Redundancy q1	Rank	-0.07455	0.027	0.545
Naïve Representativeness q1	Rank	0.16713	0.04678	0.0778
Similarity-sensitive Alpha q0	Rank	-0.007401	0.011962	2.17E-05
Similarity-sensitive Alpha q1	Rank	-0.03117	0.01654	0.000117
Similarity-sensitive Gamma q1	Rank	-0.052428	0.008861	0.113548
Similarity-sensitive Redundancy q1	Rank	-0.2204	0.0436	0.00263
Similarity-sensitive Representativeness q1	Rank	0.02126	0.0127	0.0803
Naïve Alpha q0	Rank	0.11	0.04	0.00791
	UTM Coordinates South	0.00	0.00	0.28417
Naive Alpha q1	Rank	0.04	0.03	0.2266
	UTM Coordinates South	0.00	0.00	0.0178
Naïve Redundancy q1	Rank	-0.08	0.03	0.0141
	UTM Coordinates South	0.00	0.00	0.5295
Naïve Redundancy q1	Rank	0.00	0.05	0.993
	UTM Coordinates East	0.00	0.00	0.13

Table S5.5 Results of the Moran's I test for spatial autocorrelation. A test of spatial autocorrelation was performed on the residuals of the linear models presented in Table S5.4. Where there was evidence of possible spatial autocorrelation, the models were re-run to include the spatial coordinates.

Response	Explanatory Variable	Observed	Expected	SD	p	Obs.Stat
Naïve Alpha q0	Rank	0.1464629	-0.05882	0.092771	0.026909	0.24286
Naive Alpha q1	Rank	0.1285657	-0.05882	0.093006	0.043926	0.18739
Naïve Gamma q1	Rank	-0.1313312	-0.05882	0.093111	0.436144	-0.07251
Naïve Redundancy q1	Rank	-0.2692966	-0.05882	0.086793	0.015308	-0.24197
Naïve Representativeness q1	Rank	-0.0350582	-0.05882	0.077264	0.758397	0.023765
Similarity-sensitive Alpha q0	Rank	-0.1622093	-0.05882	0.090216	0.251805	-0.10339
Similarity-sensitive Alpha q1	Rank	-0.1460772	-0.05882	0.08661	0.31373	-0.08725
Similarity-sensitive Gamma q1	Rank	-0.1105223	-0.05882	0.09453	0.584447	-0.05147
Similarity-sensitive Redundancy q1	Rank	0.08524112	-0.05882	0.088567	0.103816	0.14406
Similarity-sensitive Representativeness q1	Rank	-0.05456628	-0.05882	0.082435	0.958813	0.00257
Naïve Alpha q0	Rank + UTM Coordinates South	0.0400761	-0.05882353	0.09334274	0.2894	0.10889
Naive Alpha q1	Rank + UTM Coordinates South	-0.04211296	-0.05882353	0.08558695	0.8452	0.01671
Naïve Redundancy q1	Rank + UTM Coordinates South	-0.2793251	-0.05882353	0.0884537	0.0127	-0.2205
Naïve Redundancy q1	Rank + UTM Coordinates East	-0.2071293	-0.05882353	0.08942062	0.0972	-0.14831

Table S5.6 List of light loving species excluded from dataset for alternative analysis as described in section 5.3.3.

Species
Adelpha cytherea
Harjesia blanda
Hermeuptychia fallax
Hermeuptychia sp.
Satyrinae sp.
Urbanus proteus
Historis odius
Narope syllabus
Pareuptychia ocirrhoe
Tithorea harmonia

8.5 Chapter 6

8.5.1 Tables

Table S6.1 Results of the Spearman rank correlations tests of the correlation between the different acoustic diversity indices and disturbance at different times of day.

Time point	Variable 1	Variable 2	p	rho	rho 95% CI	
overall	ACI	Disturbance Rank	0.00000	-0.159	-0.182	-0.136
600	ACI	Disturbance Rank	0.16175	0.087	-0.031	0.203
900	ACI	Disturbance Rank	0.01649	-0.132	-0.234	-0.026
1200	ACI	Disturbance Rank	0.00000	-0.264	-0.354	-0.165
1500	ACI	Disturbance Rank	0.03886	-0.113	-0.214	-0.010
1800	ACI	Disturbance Rank	0.74685	0.019	-0.101	0.136
2100	ACI	Disturbance Rank	0.00120	-0.213	-0.339	-0.083
0	ACI	Disturbance Rank	0.00067	-0.232	-0.369	-0.095
300	ACI	Disturbance Rank	0.29708	-0.073	-0.211	0.069
overall	ADiv	Disturbance Rank	0.00000	-0.166	-0.190	-0.142
600	ADiv	Disturbance Rank	0.19196	-0.081	-0.207	0.047
900	ADiv	Disturbance Rank	0.00000	-0.279	-0.376	-0.177
1200	ADiv	Disturbance Rank	0.00999	-0.140	-0.245	-0.034
1500	ADiv	Disturbance Rank	0.00398	-0.157	-0.258	-0.049
1800	ADiv	Disturbance Rank	0.00000	-0.367	-0.467	-0.258
2100	ADiv	Disturbance Rank	0.00479	-0.186	-0.320	-0.052
0	ADiv	Disturbance Rank	0.15935	-0.097	-0.231	0.037
300	ADiv	Disturbance Rank	0.03392	-0.147	-0.289	0.001
overall	AEven	Disturbance Rank	0.00000	0.154	0.130	0.178
600	AEven	Disturbance Rank	0.25753	0.071	-0.057	0.197
900	AEven	Disturbance Rank	0.00001	0.247	0.144	0.345

Time point	Variable 1	Variable 2	p	rho	rho 95% CI	Time point
1200	AEven	Disturbance Rank	0.03627	0.114	0.007	0.220
1500	AEven	Disturbance Rank	0.00832	0.144	0.037	0.248
1800	AEven	Disturbance Rank	0.00000	0.367	0.257	0.470
2100	AEven	Disturbance Rank	0.00711	0.178	0.040	0.317
0	AEven	Disturbance Rank	0.22648	0.084	-0.052	0.217
300	AEven	Disturbance Rank	0.06255	0.129	-0.018	0.270
overall	ACI	Distance to MLC	0.00000	0.085	0.050	0.120
overall	ADiv	Distance to MLC	0.53348	0.011	-0.023	0.045
overall	AEven	Distance to MLC	0.12188	-0.027	-0.061	0.006

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Table S6.2 General linear mixed models of the responses of the acoustic indices to disturbance rank and other environmental variables. Listed here are all the log-likelihoods and degrees of freedom of all GLMMs tested. In all the models, the raw index of acoustic evenness was used (the Gini coefficient) in which high values represent low evenness.

Model	Log Likelihood (ML)	Degrees of freedom
log(ACI_0000) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	387.8676	9
log(ACI_0000) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	393.184	8
log(ACI_0000) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	399.7666	7
log(ACI_0000) ~ Rank + Elevation + Distance to River + (1|Songmeter)	404.0822	6
log(ACI_0000) ~ Rank + Elevation + Rain + (1|Songmeter)	410.1612	6
log(ACI_0000) ~ Rank + Rain + (1|Songmeter)	416.2041	5
log(ACI_0000) ~ Elevation + Rain + (1|Songmeter)	412.811	5
log(ACI_0900) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	662.1874	9
log(ACI_0900) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	662.6767	8
log(ACI_0900) ~ Rank + Elevation + Distance to River + Rain + Temperature + (1|Songmeter)	660.8165	8
log(ACI_0900) ~ Rank + Elevation + Distance to River + Humidity + Temperature + (1|Songmeter)	668.6085	8
log(ACI_0900) ~ Rank + Elevation + Humidity + Temperature + (1|Songmeter)	672.8209	7
log(ACI_0900) ~ Rank + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	674.2429	7
log(ACI_0900) ~ Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	673.5925	7
log(ACI_1200) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	673.3201	9
log(ACI_1200) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	678.5966	8
log(ACI_1200) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	677.4223	7

Continued below

Model	Log Likelihood (ML)	Degrees of freedom
log(ACI_1200) ~ Rank + Elevation + Distance to River + Humidity + (1|Songmeter)	686.1775	7
log(ACI_1200) ~ Rank + Elevation + Humidity + (1|Songmeter)	696.1272	6
log(ACI_1200) ~ Rank + Humidity + (1|Songmeter)	705.0136	5
log(ACI_1200) ~ Humidity + (1|Songmeter)	705.9103	4
log(ACI_1500) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	734.1088	9
log(ACI_1500) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	736.9621	8
log(ACI_1500) ~ Rank + Elevation + Distance to River + Rain + Temperature + (1|Songmeter)	734.4078	8
log(ACI_1500) ~ Rank + Elevation + Distance to River + Humidity + Temperature + (1|Songmeter)	739.7749	8
log(ACI_1500) ~ Rank + Elevation + Rain + Humidity + Temperature + (1|Songmeter)	745.6899	8
log(ACI_1500) ~ Rank + Rain + Humidity + Temperature + (1|Songmeter)	754.7555	7
log(ACI_1500) ~ Rain + Humidity + Temperature + (1|Songmeter)	760.865	6
log(ACI_2100) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	437.8559	9
log(ACI_2100) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	443.4784	8
log(ACI_2100) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	449.9068	7
log(ACI_2100) ~ Rank + Elevation + Distance to River + (1|Songmeter)	454.5978	6
log(ACI_2100) ~ Rank + Elevation + Rain (1|Songmeter)	459.6916	6
log(ACI_2100) ~ Rank + Rain + (1|Songmeter)	463.5407	5
log(ACI_2100) ~ Elevation + Rain + (1|Songmeter)	460.413	5

Model	Log Likelihood (ML)	Degrees of freedom
log(ADiv_0300) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	145.4503	9
log(ADiv_0300) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	149.7495	8
log(ADiv_0300) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	155.4521	7
log(ADiv_0300) ~ Rank + Elevation + Distance to River + (1|Songmeter)	161.0731	6
log(ADiv_0300) ~ Rank + Elevation + (1|Songmeter)	171.1332	5
log(ADiv_0300) ~ Rank + (1|Songmeter)	176.816	4
log(ADiv_0900) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	244.6894	9
log(ADiv_0900) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	241.8165	8
log(ADiv_0900) ~ Rank + Elevation + Distance to River + Rain + Temperature + (1|Songmeter)	248.2183	8
log(ADiv_0900) ~ Rank + Elevation + Distance to River + Humidity + Temperature + (1|Songmeter)	250.3615	8
log(ADiv_0900) ~ Rank + Elevation + Humidity + Temperature + (1|Songmeter)	257.9194	7
log(ADiv_0900) ~ Rank + Distance to River + Humidity + Temperature + (1|Songmeter)	257.8754	7
log(ADiv_0900) ~ Distance to River + Humidity + Temperature + (1|Songmeter)	260.1328	6
log(ADiv_1200) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	285.9251	9
log(ADiv_1200) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	287.9956	8
log(ADiv_1200) ~ Rank + Elevation + Distance to River + Rain + Temperature + (1|Songmeter)	291.651	8
log(ADiv_1200) ~ Rank + Elevation + Distance to River + Temperature + (1|Songmeter)	297.3801	7
log(ADiv_1200) ~ Rank + Elevation + Temperature + (1|Songmeter)	307.8167	6
log(ADiv_1200) ~ Rank + Temperature + (1|Songmeter)	315.4253	5
log(ADiv_1200) ~ Temperature + (1|Songmeter)	320.2186	4

Model	Log Likelihood (ML)	Degrees of freedom
log(ADiv_1500) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	137.4484	9
log(ADiv_1500) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	140.6678	8
log(ADiv_1500) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	146.2093	7
log(ADiv_1500) ~ Rank + Elevation + Distance to River + (1|Songmeter)	152.0087	6
log(ADiv_1500) ~ Rank + Elevation + (1|Songmeter)	161.9651	5
log(ADiv_1500) ~ Rank + (1|Songmeter)	169.1494	4
log(ADiv_1800) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	153.5237	9
log(ADiv_1800) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	157.9116	8
log(ADiv_1800) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	163.6915	7
log(ADiv_1800) ~ Rank + Elevation + Distance to River + (1|Songmeter)	169.5511	6
log(ADiv_1800) ~ Rank + Elevation + (1|Songmeter)	179.5046	5
log(ADiv_1800) ~ Rank + (1|Songmeter)	184.1848	4
log(ADiv_1800) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	196.4933	9
log(ADiv_1800) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	200.9089	8
log(ADiv_1800) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	206.556	7
log(ADiv_1800) ~ Rank + Elevation + Distance to River + (1|Songmeter)	211.7334	6
log(ADiv_1800) ~ Rank + Elevation + (1|Songmeter)	221.365	5
log(ADiv_1800) ~ Rank + (1|Songmeter)	225.8203	4
log(AEven_0900) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	-408.3827	9
log(AEven_0900) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	-405.7564	8
log(AEven_0900) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	-402.6026	8
log(AEven_0900) ~ Rank + Elevation + Distance to River + (1|Songmeter)	-399.5617	8
log(AEven_0900) ~ Rank + Elevation + (1|Songmeter)	-394.8076	7
log(AEven_0900) ~ Rank + Distance to River (1|Songmeter)	-394.3208	7

Model	Log Likelihood (ML)	Degrees of freedom
log(AEven_0900) ~ Distance to River + (1|Songmeter)	-395.0266	6
log(AEven_1200) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	-430.9039	9
log(AEven_1200) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	-428.2582	8
log(AEven_1200) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	-426.057	7
log(AEven_1200) ~ Rank + Elevation + Distance to River + Humidity + (1|Songmeter)	-424.0185	7
log(AEven_1200) ~ Rank + Elevation + Humidity+ (1|Songmeter)	-418.0831	6
log(AEven_1200) ~ Rank + Distance to River + Humidity (1|Songmeter)	-418.5662	6
log(AEven_1200) ~ Distance to River + Humidity (1|Songmeter)	-416.1794	5
log(AEven_1500) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	-409.473	9
log(AEven_1500) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	-407.8579	8
log(AEven_1500) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	-404.3572	7
log(AEven_1500) ~ Rank + Elevation + Distance to River + (1|Songmeter)	-399.9074	6
log(AEven_1500) ~ Rank + Elevation + (1|Songmeter)	-391.76	5
log(AEven_1500) ~ Rank + (1|Songmeter)	-386.1512	4
log(AEven_1800) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	-335.6948	9
log(AEven_1800) ~ Rank + Elevation + Distance to River + Rain + Humidity + (1|Songmeter)	-333.7776	8
log(AEven_1800) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	-329.8719	7
log(AEven_1800) ~ Rank + Elevation + Distance to River + (1|Songmeter)	-325.6024	6
log(AEven_1800) ~ Rank + Elevation + (1|Songmeter)	-317.6995	5
log(AEven_1800) ~ Rank + (1|Songmeter)	-314.4796	4
log(AEven_1800) ~ Elevation + (1|Songmeter)	-318.1181	4

Model	Log Likelihood (ML)	Degrees of freedom
log(AEven_2100) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	-296.3039	9
log(AEven_2100) ~ Rank + Elevation + Distance to River + Rain + Humidity + Temperature + (1|Songmeter)	-294.8806	8
log(AEven_2100) ~ Rank + Elevation + Distance to River + Rain + (1|Songmeter)	-293.8632	7
log(AEven_2100) ~ Rank + Elevation + Distance to River + Humidity + (1|Songmeter)	-291.9378	7
log(AEven_2100) ~ Rank + Elevation + Humidity + (1|Songmeter)	-284.6162	6
log(AEven_2100) ~ Rank + Humidity + (1|Songmeter)	-288.1795	5
log(AEven_2100) ~ Elevation + Humidity + (1|Songmeter)	-282.5381	5
log(ACI) ~ Rank + distance to MLC + (1|Songmeter)	6150.868	5
log(ACI) ~ Rank + (1|Songmeter)	6161.785	4
log(ADiv) ~ Rank + distance to MLC + (1|Songmeter)	1976.497	5
log(ADiv) ~ Rank + (1|Songmeter)	1967.871	4
log(AEven) ~ Rank + distance to MLC + (1|Songmeter)	-3999.988	5
log(AEven) ~ Rank + (1|Songmeter)	-4027.117	4

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Table S6.3 Details of the estimated coefficients and p values associated with the best fitting models identified in Table S6.2.

Model	Variable	Estimated coefficient	Std Error	t value	Chi sq.	p value
log(ACI_0000) ~ Rank + Elevation + Rain + (1|Songmeter)	Rank	-0.0049	0.0021	-2.2900	5.2522	0.0219
	Elevation	0.0002	0.0001	2.2800	5.1976	0.0226
	Rain	0.0006	0.0002	2.5200	6.3403	0.0118
log(ACI_0900) ~ Rank + Elevation + Distance to River + Humidity + Temperature + (1|Songmeter)	Rank	0.0017	0.0015	1.1100	1.2331	0.2668
	Elevation	-0.0001	0.0001	-2.5400	6.4442	0.0111
	Distance to River	0.0000	0.0000	3.8800	15.0377	0.0001
	Humidity	0.0015	0.0004	3.8500	14.7963	0.0001
	Temperature	0.0034	0.0010	3.3400	11.1661	0.0008
log(ACI_1200) ~ Rank + Humidity + (1|Songmeter)	Rank	-0.0034	0.0010	-3.5000	11.9330	0.0006
	Humidity	0.0009	0.0002	4.3000	18.3620	0.0000
log(ACI_1500) ~ Rank + Rain + Humidity + Temperature + (1|Songmeter)	Rank	-0.0003	0.0008	-0.3400	0.1167	0.7327
	Rain	-0.0003	0.0002	-2.2200	4.9166	0.0266
	Humidity	0.0012	0.0003	3.8500	14.7894	0.0001
	Temperature	0.0021	0.0008	2.6000	6.7407	0.0094
log(ACI_2100) ~ Rank + Elevation + Rain (1|Songmeter)	Rank	-0.0056	0.0018	-3.1000	9.5897	0.0020
	Elevation	0.0002	0.0001	3.1500	9.8932	0.0017
	Rain	0.0005	0.0002	2.2900	5.2526	0.0219
log(ADiv_0300) ~ Rank + (1|Songmeter)	Rank	0.0018	0.0041	0.4500	0.2062	0.6498
log(AEven) ~ Rank + distance to MLC + (1|Songmeter)	Distance to MLC	-0.00004	<0.0001	-6.52	42.447	<0.0001
	Rank	-0.0297	0.0362	-8.208	67.368	<0.0001
	Distance to MLC	0.0004	<0.0001	8.648	74.794	<0.0001

Model	Variable	Estimated coefficient	Standard Error	t value	Chi sq.	p value
log(ADiv_0900) ~ Rank + Distance to River + Humidity + Temperature + (1|Songmeter)	Rank	-0.0084	0.0038	-2.2370	5.0049	0.0253
	Distance to River	0.0000	0.0000	-2.3600	5.5680	0.0183
	Humidity	0.0026	0.0014	1.8200	3.3124	0.0688
	Temperature	0.0144	0.0037	3.9530	15.6297	0.0001
log(ADiv_1200) ~ Rank + Temperature + (1|Songmeter)	Rank	-0.0008	0.0032	-0.2570	0.0659	0.7974
	Temperature	0.0073	0.0019	3.9680	15.7486	0.0001
log(ADiv_1500) ~ Rank + (1|Songmeter)	Rank	-0.0030	0.0049	-0.6200	0.3840	0.5355
log(ADiv_1800) ~ Rank + Elevation + (1|Songmeter)	Rank	-0.0107	0.0067	-1.6030	2.5687	0.1090
	Elevation	-0.0006	0.0002	-2.3860	5.6909	0.0171
log(ADiv_1800) ~ Rank + Elevation + (1|Songmeter)	Rank	0.0040	0.0052	0.7620	0.5800	0.4463
	Elevation	-0.0005	0.0002	-2.5960	6.7370	0.0094
log(AEven_0900) ~ Rank + Distance to River + (1|Songmeter)	Rank	0.0734	0.0282	2.6020	6.7707	0.0093
	Distance to River	0.0003	0.0001	2.9430	8.6614	0.0033
log(AEven_1200) ~ Rank + Distance to River + Humidity + (1|Songmeter)	Rank	0.0205	0.0283	0.7250	0.5263	0.4682
	Distance to River	0.0002	0.0001	2.3740	5.6342	0.0176
	Humidity	0.0120	0.0061	1.9580	3.8326	0.0503
log(AEven_1200) ~ Rank + (1|Songmeter)	Rank	0.0687	0.0267	2.5720	6.6155	0.0101
log(AEven_1200) ~ Rank + Elevation + (1|Songmeter)	Rank	0.0948	0.0398	2.3820	5.6751	0.0172
	Elevation	0.0033	0.0015	2.2060	4.8669	0.0274
log(AEven_1200) ~ Rank + Humidity + (1|Songmeter)	Rank	0.1667	0.0337	4.9490	24.4895	0.0000
	Humidity	-0.0124	0.0075	-1.6440	2.7019	0.1002
log(ACI) ~ Rank + (1|Songmeter)	Rank	0.0045	0.0008	5.3	28.154	<0.0001
log(ADiv) ~ Rank + distance to MLC + (1|Songmeter)	Rank	0.0032	0.0055	5.72	32.739	<0.0001

Table S6.4 Moran's I test for spatial autocorrelation in best fitting GLMMs detailed in Table S6.3.

Model	observed	expected	Obs-Exp	sd	p
log(ACI_0000) ~ Rank + Elevation + Rain + (1|Songmeter)	-0.0031	-0.0048	0.0017	0.0082	0.8364
log(ACI_0900) ~ Rank + Elevation + Distance to River + Humidity + Temperature + (1|Songmeter)	-0.0079	-0.0030	-0.0049	0.0051	0.3410
log(ACI_1200) ~ Rank + Humidity + (1|Songmeter)	-0.0124	-0.0030	-0.0095	0.0051	0.0652
log(ACI_1500) ~ Rank + Rain + Humidity + Temperature + (1|Songmeter)	-0.0211	-0.0030	-0.0182	0.0050	0.0003
log(ACI_2100) ~ Rank + Elevation + Rain (1|Songmeter)	-0.0287	-0.0044	-0.0243	0.0075	0.0011
log(ADiv_0300) ~ Rank + (1|Songmeter)	-0.0062	-0.0048	-0.0013	0.0080	0.8681
log(ADiv_0900) ~ Rank + Distance to River + Humidity + Temperature + (1|Songmeter)	-0.0121	-0.0030	-0.0091	0.0051	0.0733
log(ADiv_1200) ~ Temperature + (1|Songmeter)	-0.0278	-0.0030	-0.0248	0.0051	0.0000
log(ADiv_1500) ~ Rank + (1|Songmeter)	-0.0400	-0.0030	-0.0371	0.0049	0.0000
log(ADiv_1800) ~ Rank + Elevation + (1|Songmeter)	-0.0058	-0.0036	-0.0023	0.0059	0.7041
log(ADiv_1800) ~ Rank + Elevation + (1|Songmeter)	-0.0356	-0.0044	-0.0312	0.0072	0.0000
log(AEven_0900) ~ Rank + Distance to River (1|Songmeter)	-0.0374	-0.0030	-0.0344	0.0052	0.0000
log(AEven_1200) ~ Rank + Distance to River + Humidity (1|Songmeter)	-0.0178	-0.0030	-0.0148	0.0052	0.0040
log(AEven_1200) ~ Rank + (1|Songmeter)	-0.0374	-0.0030	-0.0344	0.0050	0.0000
log(AEven_1200) ~ Rank + Elevation + (1|Songmeter)	-0.0096	-0.0036	-0.0060	0.0060	0.3159
log(AEven_1200) ~ Rank + Humidity + (1|Songmeter)	-0.0424	-0.0044	-0.0380	0.0076	0.0000

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